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THE EARLY STAGES OF THE DEVELOPMENT OF THE PERICARDIUM. By Arthur Robinson, M.D., M.R.C.S., *Professor of Anatomy, King's College, London.* (Plates I., II.)

THE development of the pericardium has usually been considered in association with the development of the great veins and with the development of the diaphragm. In consequence of this much stress has been laid upon phenomena which have no direct bearing upon the formation of the pericardium itself, and the essential simplicity of the process has been obscured, to a certain extent, by the use of terms which are not in all cases appropriate, and in many are misleading. As a result a large amount of misconception exists with regard to the details of the formation of this important serous sac in mammals, and this misconception is mainly due to inaccurate descriptions of the mode in which the embryo is evolved from the surface of the ovum.

The incorrect descriptions most responsible for the misunderstanding are those which ascribe the demarcation of the embryo and its separation from the non-embryonic part of the ovum as due to the formation of sulci, which appear round the margins of the embryonic area and gradually converge beneath it to form the boundary of a continually narrowing orifice—the umbilical orifice; in other words, to descriptions which lead their readers to infer that the embryo is demarcated by a process of tucking off from the ovum, whilst at the same time it is moulded into its proper form.

In association with this misconception of the manner in which the embryo is separated from the remainder of the ovum,

a description of the early stages of the development of the pericardium is given which, at first sight, is apparently in accordance with the appearances observed in transverse sections of developing ova; but when the examination of such sections is controlled by the observation of longitudinal sections in similar stages of development, then it is found that the appearances seen in transverse sections are deceptive, and that the phenomena observed are capable of a different interpretation to that previously placed upon them.

It has been shown by the examination of transverse sections that, whilst the embryonic area is still outspread upon the upper part of the ovum, the mesoderm within its margins becomes cleft into an outer or somatic and an inner or splanchnic layer, but that in the antero-lateral parts of the area this cleavage of the mesoderm does not extend either to the margins of the area or
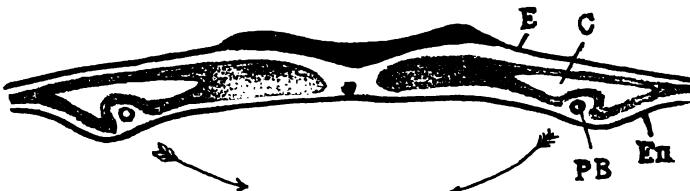
Fig. 1.

to the sides of the neural groove, and that, consequently, on each side a mesodermal tube is formed, and in the lower or splanchnic layer of each of these tubes a longitudinal vessel appears which has been described as a rudiment of the heart (fig. 1). The examination of sections of this kind, and the preconceived idea that the folds of the embryo are formed by a process of tucking in of the margins of the embryonic area, have led to the statement that, as the lateral folds pass inwards beneath the growing embryo and approach the mid-ventral line, the two mesodermal tubes meet together and divide the anterior portion of the blastodermic cavity into two parts, an upper (the foregut), and a lower (the anterior part of the yolk sac), and that the so-called rudiments of the heart, which lie in the inner walls of the mesodermal tubes, also fuse at the same time to form a single median heart (fig. 2). Obviously, at the period under consideration, a heart developed in such a manner would be attached for

a time by a fold of mesoderm to the foregut dorsally, and to the yolk sac ventrally, but the idea that the lateral folds of the embryo are converging ventrally has been held so tenaciously as to establish the belief that the superficial ectodermal covering of the folds also reaches the middle line; otherwise, it is impossible to account for the statement which constantly reappears, that after the lateral folds have converged and the pericardial tubes have met beneath the ventral wall of the foregut, the heart is not only attached by a dorsal mesentery to the foregut, but also by a ventral mesentery to the ventral wall of the body.   In later stages, it is obvious that no ventral mesentery exists, for the pericardial sac is not divided, and it is asserted
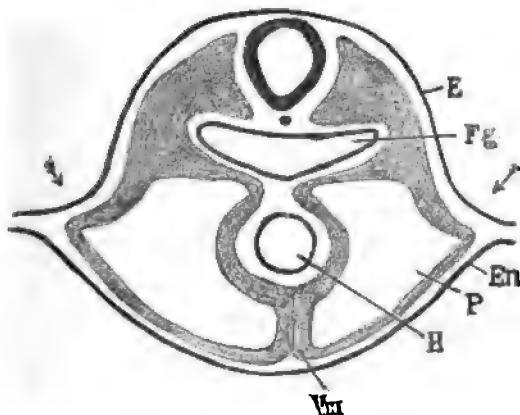
FIG. 2.

that this undivided condition of the pericardium is due to the disappearance of the ventral mesentery.

It may be stated at once, after the above account of the very general belief which exists regarding the early stages of the development, that the phenomena described do not occur, for they would necessitate that the ventral wall of the body from the umbilicus to the mouth is, at some period, cleft in the middle line, and that the cleft only disappears as the two lateral folds converge and separate the foregut from the remainder of the blastodermic cavity.   In no vertebrate is any such condition found.   The ectoderm and entoderm of the anterior part of the ventral wall of the body, the part in front of the umbilicus, are

never cleft in the middle line; but the mesoderm, which is a
later formation, enters this section of the body in a different
manner and at different periods of development in various groups
of animals. In this respect, the anterior part of the ventral
wall of the body, the part in front of the umbilicus, differs
essentially from the posterior part, the part behind the um-
bilicus, for the former is developed from the portion of the
ovum which lies in front of and below the blastoporic region,
and the latter is formed from the primitive streak which repre-
sents the closed blastopore. The anterior part, therefore, was
never cleft mesially, whilst the posterior was; and the latter may,
and, not uncommonly, does revert to its open condition, such re-
opening resulting, in certain cases, in extroversion of the bladder.
It is the want of appreciation of these facts, combined with a
false idea regarding the mode of formation of the folds of the
embryo, which has led to the incorrect descriptions of the
formation of the pericardium in mammals, for in these
vertebrates the pericardium is never separated into right
and left halves by a ventral mesocardium; indeed, in
them a ventral mesocardium does not exist; and although
it is present in other groups, it is not formed in the manner
usually described.

Before the early stages of the development of the pericardium
in mammals can be properly appreciated, its formation in other
vertebrates must be investigated, and at the outset of this
investigation it is necessary to obtain a clear idea of the
relationship of the embryo to the ovum, and of the origin,
extension and differentiation of the mesoderm.

As regards the relationship of the embryo to the ovum,
vertebrates are divided into two great groups, those in which the
ovum becomes the embryo, as in Amphioxus and amphibians,
and those in which only part of the ovum becomes the embryo,
the remainder being utilised in the formation of nutritive and
protective membranes and appendages, as in reptiles, birds and
mammals.

In the simpler forms of vertebrates in which the ovum
becomes the embryo, the formation of the pericardial region
takes place in the least complicated manner.

In AMPHIOXUS the unilaminar organism which results from

the segmentation of the ovum is converted into a bilaminar in-
dividual by invagination, and the invagination cavity becomes
the alimentary or enteric cavity of the embryo. The aperture
which leads into the enteric cavity is the primitive mouth or
blastopore; it becomes elongated from before backwards, and
immediately below its margins a series of pocketlike diverticula
are projected outwards into the remains of the segmentation
cavity. These diverticula are the rudiments of the mesoderm
(fig. A), and the cavities contained within them are the rudiments
of the cœlom or body cavity. The diverticula gradually grow
towards the ventral aspect of the embryo, and finally they meet
beneath the ventral wall of the alimentary canal, where the
adjacent walls of the cœlomic rudiments of opposite side fuse
together and form, for a time, a mesentery. In the dorsal part
of this mesentery a subintestinal blood-vessel is developed, which
represents, in the anterior part of its extent at least, the heart
of the higher forms. Therefore in Amphioxus the representative
of the heart of the higher vertebrates is connected with the
ventral wall of the body by a ventral mesentery, which exists for
a considerable time.

IN AMPHIBIA the process of invagination and the formation
of the blastopore and enteron are more complicated than in
Amphioxus, and the mesoderm is formed simultaneously with
the entoderm. Ultimately, however, it is delaminated from the
entoderm, and cleft into outer and inner layers, by the appearance
within it of the cœlomic space. As in Amphioxus the mesodermal
sheets of opposite sides meet together beneath the ventral wall of
the alimentary canal, where they form for a time a mesentery
(figs. B and C). Beneath that part of the alimentary canal
which afterwards becomes the pharynx the heart appears in the
dorsal border of the mesentery, and the cœlomic spaces in its
immediate neighbourhood become converted into the pericardium.
In the early stages, therefore, in the tadpole, the two halves of
the pericardial section of the cœlom are separated from each
other by the ventral mesentery which connects the heart with
the ventral wall of the body.   .

IN REPTILES, BIRDS, AND MAMMALS, the processes of develop-
ment are much more complicated, for the ovum is no longer
utilised for the formation of the embryo alone, but also for the

formation of a series of membranes and appendages, which are endowed with protective and nutritive functions, and the two parts, though they are merely segments of one continuous surface, are soon differentiated from each other, so that at a very early period of development it is possible to recognise an embryonic and a non-embryonic section of the ovular surface. The margin of the embryonic section is clearly defined, and from the time of its appearance to the end of life it can always be easily recognised, for it is the margin of the umbilical orifice, which increases until birth, and then is only reduced by a process of cicatrisation, for it is obvious that the diameter of the embryonic area of the ovum is much smaller than the diameter of the umbilical orifice of the adult body. Therefore the orifice is not reduced in size during the early stages of development by the convergence of its margins towards a central point. This being the case, no tucking off of the embryo from the surface of the ovum can occur; on the contrary, what does occur is almost the exact opposite of such a process, for the margin of the area remains as a relatively slow-growing region, whilst the embryonic and the extra-embryonic portions of the wall of the ovum rapidly increase in extent. Under these circumstances, it follows that the margin of the embryonic area will soon appear as a ring between the upper or embryonic and the lower or extra-embryonic parts of the ovum, both of which have expanded beyond it in all directions.

In the consideration of the development of the pericardium, the embryonic region alone requires further study, and it becomes necessary to inquire into its mode of growth, but before this can be appreciated, the positions of certain sections of the embryonic region must be defined.

The embryonic area is at first circular, then ovoid, and finally pear-shaped (fig. D). The narrow end of the pear-shaped area is posterior, and upon it appears a linear thickening, the primitive streak. In front of the primitive streak the neural folds are formed; their posterior ends embrace the anterior part of the primitive streak; and·their anterior ends unite together some distance behind the anterior end of the embryonic area. In the meantime the mesoderm has extended from the sides and posterior extremity of the primitive streak, which represents the fused lips

of the blastopore of Amphioxus, throughout the embryonic and extra-embryonic areas, except in certain regions which vary in extent in different classes of vertebrates and also in different groups of each class.   For purposes of the present study, it is permissible to take an imaginary form in which it may be supposed that the mesoderm has extended over the whole area of the ovum between the two primitive layers, except in the middle line of the embryonic area below the mesial axis of the neural groove, and in a small area, for which I have proposed the term *bucco-pharyngeal membrane,* which is situated in front of the neural groove, and which afterwards becomes the septum between the primitive mouth and the primitive pharynx.   It may also be supposed that the mesoderm has become cleft into an outer and an inner layer, except along the margins of the neural groove on each side, where the outer and inner layers are continuous with each other (figs. J, K, L, M, N). Turning again to the embryonic area, it must be noted that the anterior portion of the region which is situated between the bucco-pharyngeal region and the anterior margin of the area is the part which will ultimately lie immediately in the anterior boundary of the umbilical orifice; it is therefore the region in which the pericardium will be developed, and may be termed the *pericardial area.*

In the early stages the pericardial region occupies the most anterior part of the embryonic area, and in the imaginary specimen under consideration it consists of the four usual layers of the germ—two outer layers, the ectoderm and the somatic mesoderm ; two inner, the entoderm and the splanchnic mesoderm ; and between the somatic and splanchnic mesoderm there is a portion of the cœlom or body cavity (figs. K, L). The main blood-vessels of the embryo have in the meantime commenced their development, and they form two longitudinal trunks, one on each side, which pass backwards in the splanchnic mesoderm from the vascular area on the wall of the yolk sac in front of the embryonic area to the vascular area behind the embryonic region ; and the vascular circle on each side is com-pleted by the capillary vessels of the vascular area, through which the blood is returned from the posterior to the anterior end of the germ.   At this period, therefore, in this imaginary

embryo, the main blood-vessel on each side would pass backwards in the splanchnic mesoderm which forms the lower or ventral boundary of the pericardial section of the cœlom (figs. J, K, L).

The first change of importance which takes place in the further development of the pericardial section of the embryo is its reversal, or the alteration of the positions of its extremities and surfaces, the primitive anterior boundary becoming the posterior, and the original ventral surface becoming the dorsal surface (figs X, Y, Z, Z_1). As this change of position is due entirely to the manner in which the embryonic area grows, it becomes necessary to consider that growth more carefully; and when embryonic areas of gradually increasing size are carefully examined, it is found that the rate of growth varies considerably in different parts of the area, and that the antero-posterior increase is more rapid than the transverse. It is in the region of the anterior end of the primitive streak that the most rapid antero-posterior growth occurs, and this section of the embryonic area constitutes a kind of nodal point. It follows, therefore, that as the margins of the embryonic area are comparatively stationary, whilst the region within the margins is rapidly growing, that the area must fold, and folding, it might project inwards into the interior of the ovum, forming a hollow invaginated tube; or upwards from the ovular surface; or forwards, backwards, and laterally over its own margins.

The folding inwards or invagination does actually occur in the very early stages of development of rats, mice, squirrels, guinea-pigs, and apparently, to a slight extent, in the human ovum, producing what is known as the inversion of the layers. The upward folding does not occur, being prevented by the walls of the cavity in which the ovum lies, but the peripheral folding occurs in all animals as the embryo is gradually moulded into form, and the preliminary inversion, if it has occurred, disappears. Thus it becomes evident that there is no tucking inwards of the margin of the embryonic area; on the contrary, the head, tail, and lateral folds, which appear as the embryo gradually assumes its form, are due to the relatively stationary condition of the margin of the area and the rapid increase of its surface extent, the two factors combined necessarily giving

rise to a folding of the area. Further, as the embryonic area increases in size it also increases in weight, and the increased weight causes it to sink into the interior of the ovum, thus producing around it a second series of folds of the extra-embryonic portion of the ovular surface which constitute the amnion folds. As the amnion folds have no bearing upon the development of the pericardium they need no further consideration, but the folds of the embryonic area have a direct bearing upon the subject of this study, and they require, therefore, more detailed investigation.

It has already been stated that the antero-posterior increase of the embryonic region is more rapid than the lateral increase, and this is soon rendered evident by the preponderance of the head fold over the lateral body folds (figs. X, Y). During the development of the head fold the anterior margin of the embryonic area remains relatively stationary, and the anterior end of the neural groove passes rápidly forwards till it projects well above and beyond the anterior end of the area. As this projection occurs, the posterior ends of the bucco-pharyngeal and pericardial regions are pushed forwards, and their surfaces are necessarily reversed. When the alteration of position is completed, what was originally the ventral surface of the pericardial region has become the dorsal surface, and it forms the ventral wall of the foregut, which is the portion of the blastodermic cavity carried forward into the embryo during the formation of the head fold (fig. X). The foregut, therefore, lies entirely within the head fold, and consequently the formation of its ventral wall cannot in any way be due to the convergence and fusion of lateral folds. In the imaginary embryo at present under consideration it is obvious that, after the formation of the head fold, the two main blood-vessels which passed backwards into the embryo from the anterior part of the vascular area must now ascend in the anterior boundary of the umbilical orifice and turn forwards in the splanchnic mesoderm of the dorsal boundary of the pericardial section of the cœlom to the lower end of the bucco-pharyngeal region, and that they will ascend from the pericardial region in the rudimentary mandibular arches which are developing along the lateral margins of the bucco-pharyngeal area to the under surface of the head (fig. X),

where they will turn backwards, towards the caudal region of the body of the embryo, under the paraxial mesoderm at the sides of the neural tube, which has been formed in the meantime by the incurvation and fusion of the margins of the neural groove (fig. Z). Subsequently, the two primitive vessels fuse together in the splanchnic mesoderm of the dorsal wall of the pericardial portion of the cœlom and project downwards into the cavity, being suspended from the dorsal wall by a mesocardium posterius, but it is perfectly obvious that under the conditions defined no ventral or anterior mesocardium can be produced, and that the pericardium is not formed by the convergence of cœlomic spaces which lie in the lateral folds and their fusion in the ventral middle line, but that it is produced by the inclusion of the anterior portion of the cœlomic space in the body as the head fold is projected forwards in association with the rapid antero-posterior increase of the embryonic area.

So far, however, only an imaginary ovum has been considered, in which the primitive blood-vessels occupy what may be considered to be their original positions and form two vascular circles, one immediately to either side of the middle line, both in the embryonic and the extra-embryonic portions of the ovum. This simple condition no longer exists, if indeed it was present at any time, either in reptiles, birds, or mammals, and the modifications of it which appear in all three groups are associated with differences in the rate of extension of the mesoderm between the two primitive layers, and to differences in its rate of cleavage into somatic and splanchnic portions. These differences are, in their turn, associated with modifications of pericardial development which are of considerable interest, and which have been very imperfectly described.

Reptiles and birds do not differ essentially from each other so far as the peculiarities of mesoderm extension are associated with the early stages of the formation of the pericardium, and birds, therefore, may be used to illustrate the phenomena which are of importance, inasmuch as they are more easily obtainable, and their development is better known than that of reptiles.

BIRDS.—

In birds, as in mammals, the mesoderm extends from the

sides and posterior end of the primitive streak, and not only does it leave the notochordal and bucco-pharyngeal portions of the embryonic area uninvaded, but also, for a considerable time, a large area which extends forwards and outwards from the bucco-pharyngeal region well into the extra-embryonic part of the ovum in front of the embryonic area (fig. D). The embryonic portion of this mesoderm-free region is that in which the pericardium will afterwards be developed, and the extra-embryonic portion subsequently becomes bent over the head of the embryo as the anterior amnion fold, which is known as the proamnion because it consists only of ectoderm and entoderm, whilst a true amnion fold is formed by a fold of the somatopleure, that is by a layer of ectoderm lined internally by a layer of somatic mesoderm. Clearly, therefore, as the primitive blood-vessels are developed in the splanchnic mesoderm, they can only pass from the anterior part of the vascular area round the margins of the proamnion and along the sides of the bucco-pharyngeal area into the embryo, and in the early stages no blood-vessels are present in the pericardial region of the ovum. At a later period the mesoderm extends both into the pericardial region and into the proamnion, and cleaves as it extends, but before this occurs the head fold is formed by the rapid antero-posterior increase of the embryonic area, and thus for a time, in birds, the whole of the ventral wall of the foregut consists of ectoderm and entoderm alone (fig. E). Subsequently, the two layers of the mesoderm, inclosing between them the cœlomic space, sweep into it from the sides, carrying with them the rudiments of the heart, which thus eventually lies in the ventral wall of the foregut, and is connected dorsally with the wall of the gut by a dorsal mesocardium, and ventrally with the ventral wall of the body by a ventral mesocardium (figs. G, H). In birds, therefore, as in amphibians, a ventral mesocardium is present; nevertheless, only the mesodermal portion of the ventral wall of the foregut is formed by the ingrowth and fusion of lateral folds. The ectoderm and entoderm belong entirely to the primitive head fold, and they are at no time cleft or separated into lateral halves in the ventral middle line. The mesoderm alone, on account of its peculiar mode of extension between the primitive layers, is cleft mesially, and it does not enter the region of the

ovum which becomes the ventral wall of the foregut until the head fold has been formed.

MAMMALS.—

In mammals, either on account of the smaller size of the ovum or on account of the more rapid extension of the mesoderm, the latter layer has extended through the pericardial section of the embryonic area, and is cleft into somatic and splanchnic layers *before* the head fold is formed, and in the earlier stages the pericardial mesoderm of these animals forms a crescentic mass, bounded in front by the anterior margin of the embryonic area and the posterior margin of the proamnion, if the latter is present, and behind by the bucco-pharyngeal membrane, whilst postero-laterally it is continuous with the general mass of the mesoderm, both of the body of the embryo and of the extra-embryonic area, at the level of the posterior part of the bucco-pharyngeal membrane (figs. O, P). In man, where apparently no proamnion is formed, and in some rodents where the proamnion is a very small and transitory structure, the mesoderm of the peri-cardial region is in close association, at the anterior border of the embryonic area, with the more anteriorly situated extra-embryonic mesoderm, but the two portions are always definitely separated by a cleft, and in these mammals, as in those which are provided with a comparatively large proamnion, the only connection of the pericardial with the non-pericardial portion of the mesoderm is situated posteriorly, on each side, at the level of the posterior part of the bucco-pharyngeal membrane. Why this separation of the anterior border of the pericardial meso-derm from the adjacent extra-embryonic mesoderm persists at the anterior border of the embryonic area in those animals in which no proamnion is present is not clear, and it can only be looked upon as an indication of the descent of the animals in question from proamniotic ancestors.

In mammals provided with a proamnion it is obvious that, as in birds, the blood-vessels passing from the anterior part of the vascular area to the embryo must run along the margins of the proamniotic membrane, and then turn forwards in the splanchnic mesoderm of the pericardial tube towards the anterior end of the embryonic region, where they turn backwards along the

sides of the bucco-pharyngeal membrane, and pass to the posterior end of the embryo beneath the paraxial mesoderm of the head and body (figs. O, R). At the posterior end of the embryonic area they enter the posterior part of the vascular area and join the capillaries, by means of which the vascular circle on each side of the ovum is completed, and they run a corresponding course in mammals in which the proamnion is rudimentary.

As the head fold develops, the posterior end of the pericardial region is swung forward, the surfaces of the region are reversed, and it is carried into the ventral wall of the developing foregut, consequently the two primitive blood-vessels of the embryo, which previously ran backwards from the anterior border of the pericardial region to the sides of the bucco-pharyngeal membrane, now run forwards from the posterior part of the reversed pericardial region to the lower. border of the reversed bucco-pharyngeal membrane, and they lie close together in the dorsal wall of the pericardial cavity, attached to the ventral wall of the foregut by a dorsal mesentery, but their ventral surfaces are free, and quite devoid of a ventral meso-cardium (figs. S, T).

At this period the fused somatic and splanchnic mesoderm of the anterior margin of the umbilicus, the original anterior border of the pericardial region, is undergoing rapid proliferation, and it forms the mass of mesodermal tissue, the septum transversum, from which the posterior wall of the pericardium and the central part of the diaphragm are afterwards differentiated. At the lateral margins of this mesoderm lie the lateral cornua of the pericardial tube, which form two small canals situated at the sides of the foregut in the anterior boundary of the umbilicus (fig. V), and in the inner and lower boundaries of these tubes, in the septum transversum, lie what were the anterior extremities of the primitive blood-vessels of the embryo, which have now become the vitelline veins. They ascend from the yolk sac into the lateral part of the anterior boundary of the umbilicus, and then pass forwards through the septum transversum at the sides of the posterior part of the foregut to the posterior part of the heart, for by this time those parts of the primitive blood-vessels which lie in the dorsal wall of the pericardium are fusing to form the single tubular heart (fig. W). It is the relation of the

lateral cornua of the pericardial tubes to the wall of the foregut
at this period which have given rise to the erroneous descriptions
of the completion of the ventral wall of the foregut by the fusion
of the ventral ends of the lateral folds of the body wall, and of
the formation of the pericardium by the union in the ventral
middle line of the portions of the cœlom which lie in each lateral
fold, such fusion necessarily producing, as in birds, a ventral
mesocardium, which disappears when the two halves of the peri-
cardial cavity become continuous. The figures which are
supposed to substantiate this interpretation of the formation of
the pericardium are simply figures of sections which pass through
the anterior boundary of the umbilical orifice, and therefore
through the primitive septum transversum and the lateral cornua
of the pericardial space, which may be called the pleuro-pericardial
canals (fig. V), as they afterwards communicate for a time with
the pleural sacs which are developed at the sides of the foregut
and dorsal to the pericardium, coincidently with the development
of the neck and the forward migration of the visceral arches; but
as these processes are associated with the later stages of the
development of the pericardium, they cannot be considered in
the present communication.

Finally, it must be noted that the pericardial region of the
embryonic area is limited anteriorly, in the early stages, by the
anterior border of the embryonic area, which becomes the anterior
boundary of the umbilicus, and that, as the pericardial region is
reversed during the formation of the head fold, the pericardium
expands so rapidly that for a time it projects backwards beyond
the ectoderm at the anterior margin of the umbilicus, and lies
between the foregut and the yolk sac, as in the ferret
(figs. AA, BB). As development proceeds, it gradually assumes
a more anterior position, and eventually lies between the fore-
gut and the ventral wall of the body, in front of the umbilical
orifice. It assumes its permanent position coincidently with
the formation of the neck and the ascent of the auricles to the
dorsal wall of the aortic bulb, but even under these circumstances
there is no ventral mesocardium.

SUMMARY.

(1) In AMPHIBIANS the pericardium is formed by the fusion of the anterior parts of the lateral halves of the cœlom in the ventral middle line beneath the anterior part of the foregut, and a ventral mesocardium is present for a time.

(2) In BIRDS the pericardium is formed after the development of the head fold by the ingrowth of the lateral parts of the cœlom into the ventral wall of the foregut and their fusion in the middle line. The rudiments of the heart lie along the dorsal part of the line of fusion, and for a time a ventral mesocardium is present.

(3) In MAMMALS the pericardial mesoderm is present in the pericardial portion of the embryonic area, and it is completely separated into somatic and splanchnic layers before the head fold appears; there is therefore a single pericardial cavity which extends from side to side along the anterior boundary of the embryonic area.

As the head fold forms, the pericardial region is reversed, and it is carried into the ventral wall of the foregut, where it forms a U-shaped tube, which communicates at each end with the general cœlom.

The rudiments of the heart are formed in the splanchnic layer of the pericardial mesoderm; therefore, after the reversal of the area, they lie in the dorsal wall of the pericardial space, attached by a dorsal mesentery to the ventral wall of the foregut, but they are never, at any time, connected with the ventral wall of the pericardium by a ventral mesocardium.

FIGURES.

(A)—diagram of the blastodermic layers in Amphioxus, showing the relation of the mesoderm to the primitive subintestinal blood-vessel.

(B)—transverse section of a tadpole, showing the formation of the two halves of the pericardial portion of the cœlom and the ventral cardiac mesentery.

(C)—transverse section of an older tadpole, showing that the

ventral cardiac mesentery disappears, and that the two halves of the pericardial portion of the cœlom fuse together.

(D)—diagram of a portion of the upper part of the ovum of a bird, showing the areas which are devoid of mesoderm and the positions in which the primitive blood-vessels will develop.

(E)—diagram of a lateral longitudinal section of the ovum of a bird, immediately after the formation of the head fold, and before the mesoderm has entered the pericardial area.

(F)—diagram of a transverse section through the embryonic portion of the ovum of a bird, along the line *a* in fig. E.

(G)—diagram of a lateral longitudinal section of the embryonic portion of the ovum of a bird, after the pericardial portion of the cœlom has extended into the embryonic area.

(H)—diagram of a transverse section of the embryonic portion of a bird's ovum, along the line *a* in fig. G.

(J)—diagram of an imaginary ovum, in which the mesoderm has extended through all parts except the floor of the neural groove and the bucco-pharyngeal region.

(K)—diagram of a lateral longitudinal section through the imaginary ovum represented in fig. J.

(L), (M), and (N)—diagrams of transverse sections of an imaginary ovum, along the lines *a*, *b*, and *c*, fig. J.

(O)—diagram of a portion of the upper part of a mammalian ovum, showing the mesoderm-free areas and the courses of the primitive blood-vessels.

(P)—diagram of a lateral longitudinal section through the ovum shown in fig O.

(Q)—diagram of a transverse section along the line *a* in fig. O.

(R)—diagram of a side view of a mammalian ovum, showing the positions of the various areas and the course of the primitive blood-vessel on the left side.

(S)—diagram of a side view of an older mammalian ovum, showing the alterations in the positions of the pericardial and bucco-pharyngeal regions, and the corresponding portions of the primitive vessels. The formation of the amnion folds on the lower or extra-embryonic part of the ovum has been omitted.

(T)—diagram of a longitudinal section of a mammalian ovum after the formation of the head and tail folds of the embryo and the formation of the amnion folds.

(U), (V), and (W)—diagrams of transverse sections of a mammalian ovum along the lines *c*, *b*, and *a* respectively in fig. T.

(X)—diagram of a lateral longitudinal section of an imaginary ovum, similar to that shown in fig. K, but after the formation of the head and tail folds, showing a continuity which never actually exists
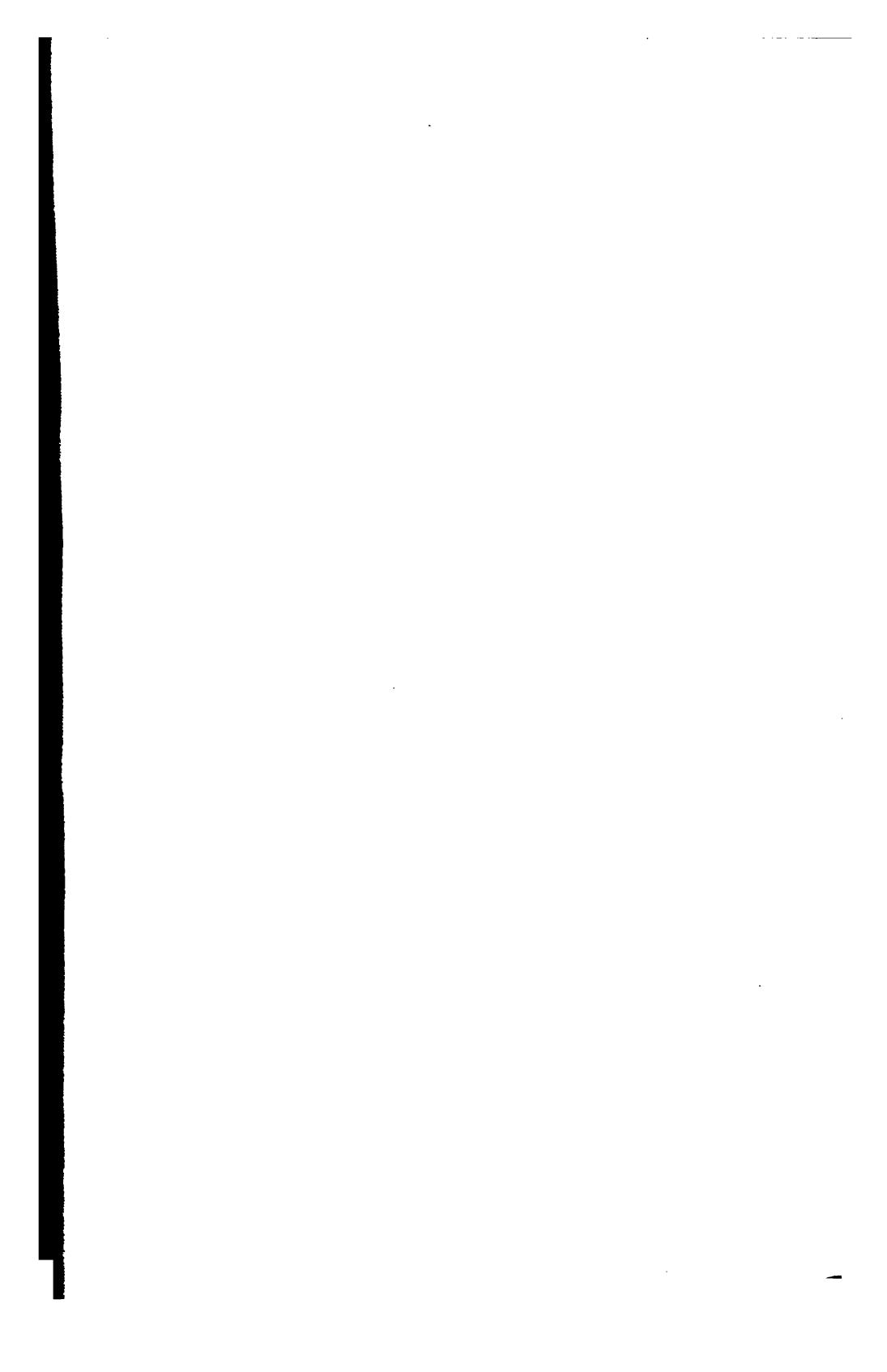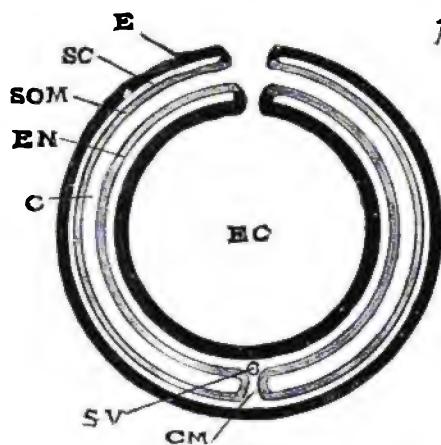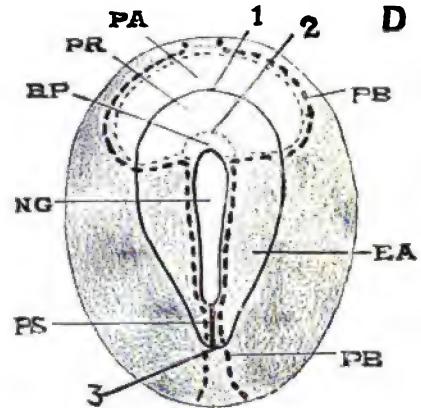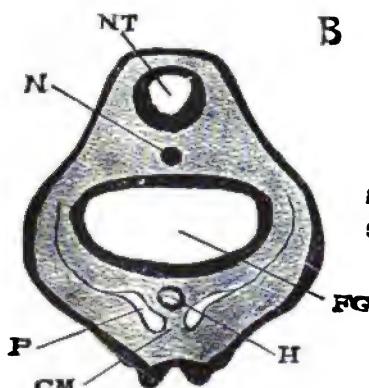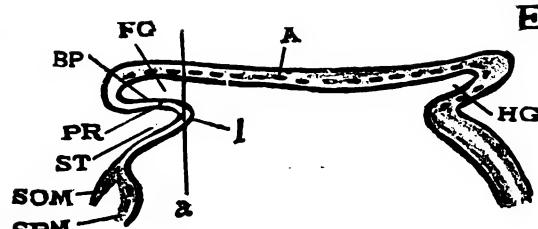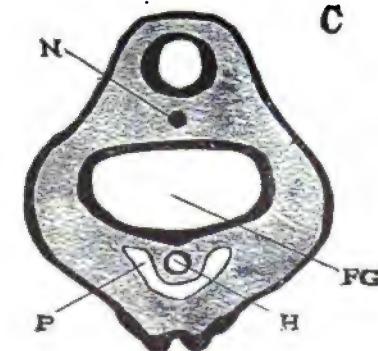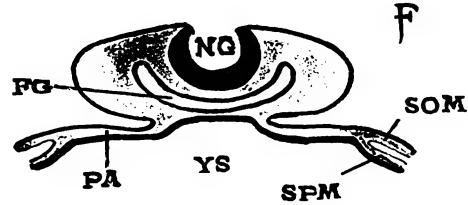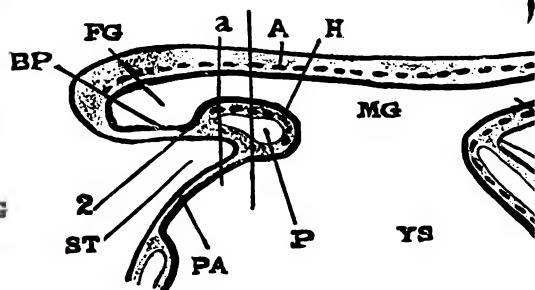
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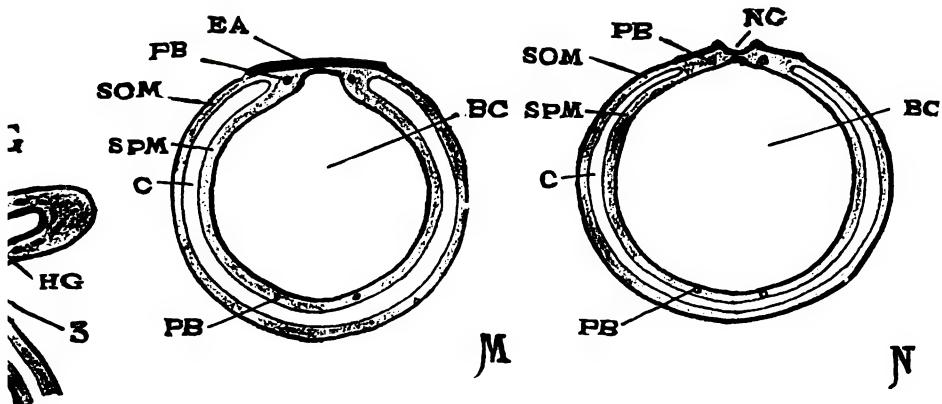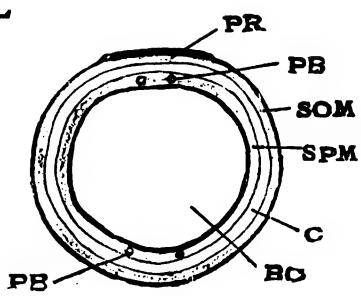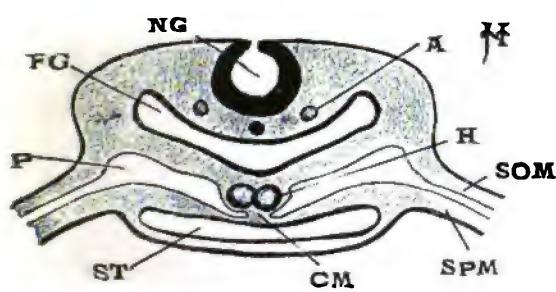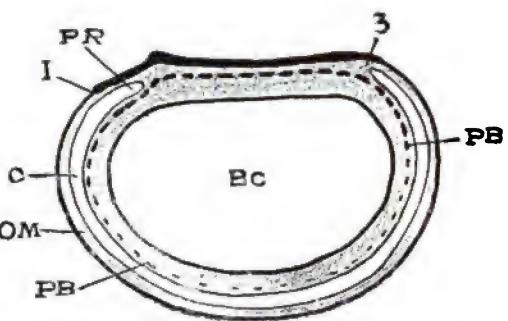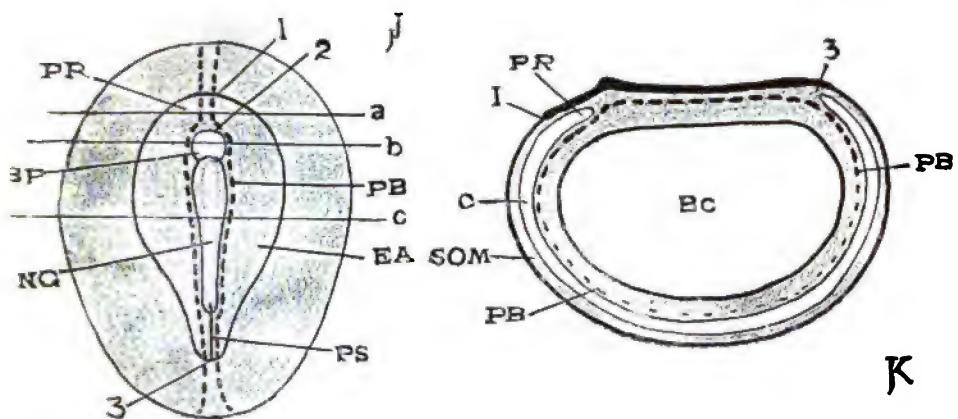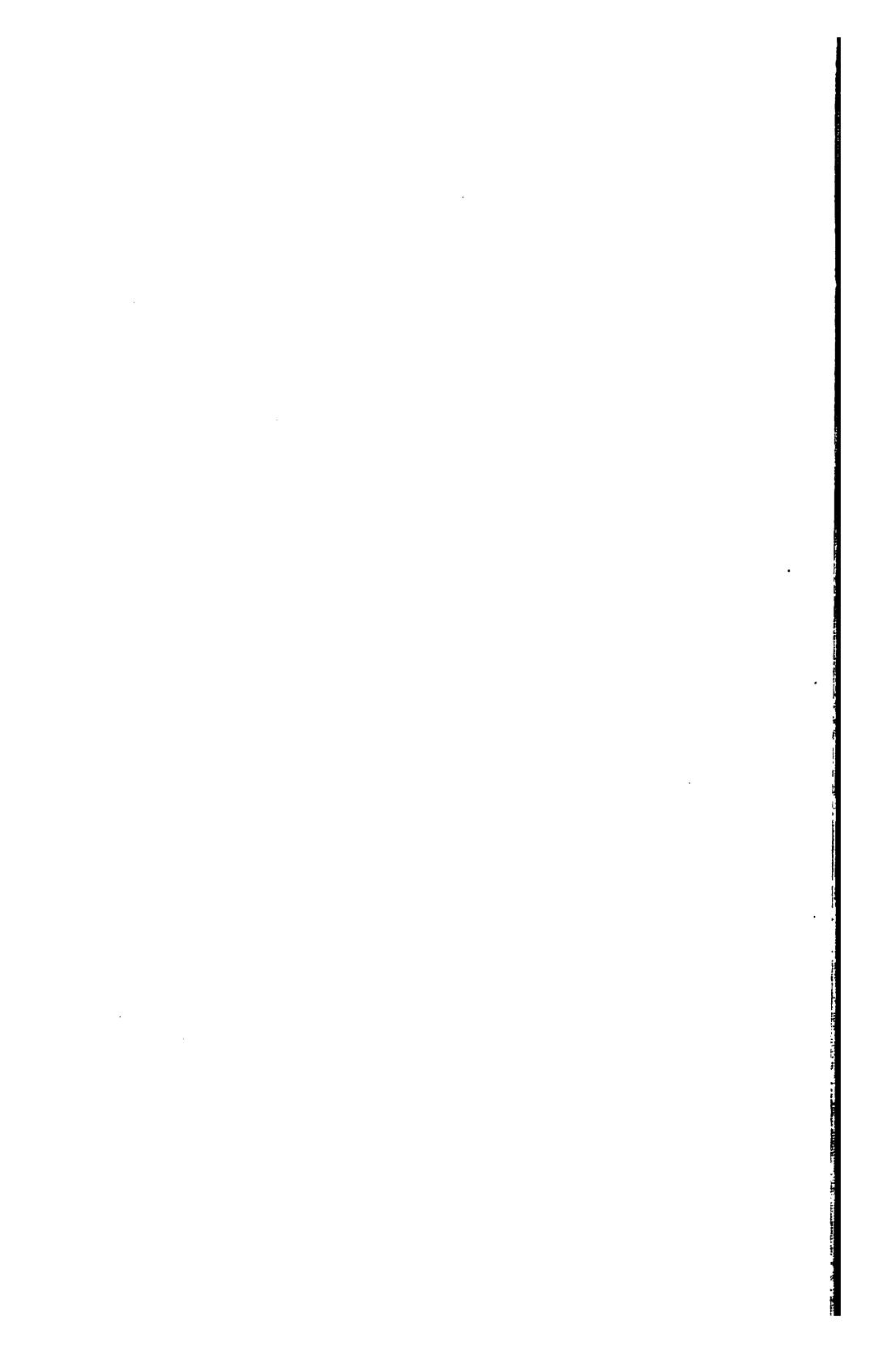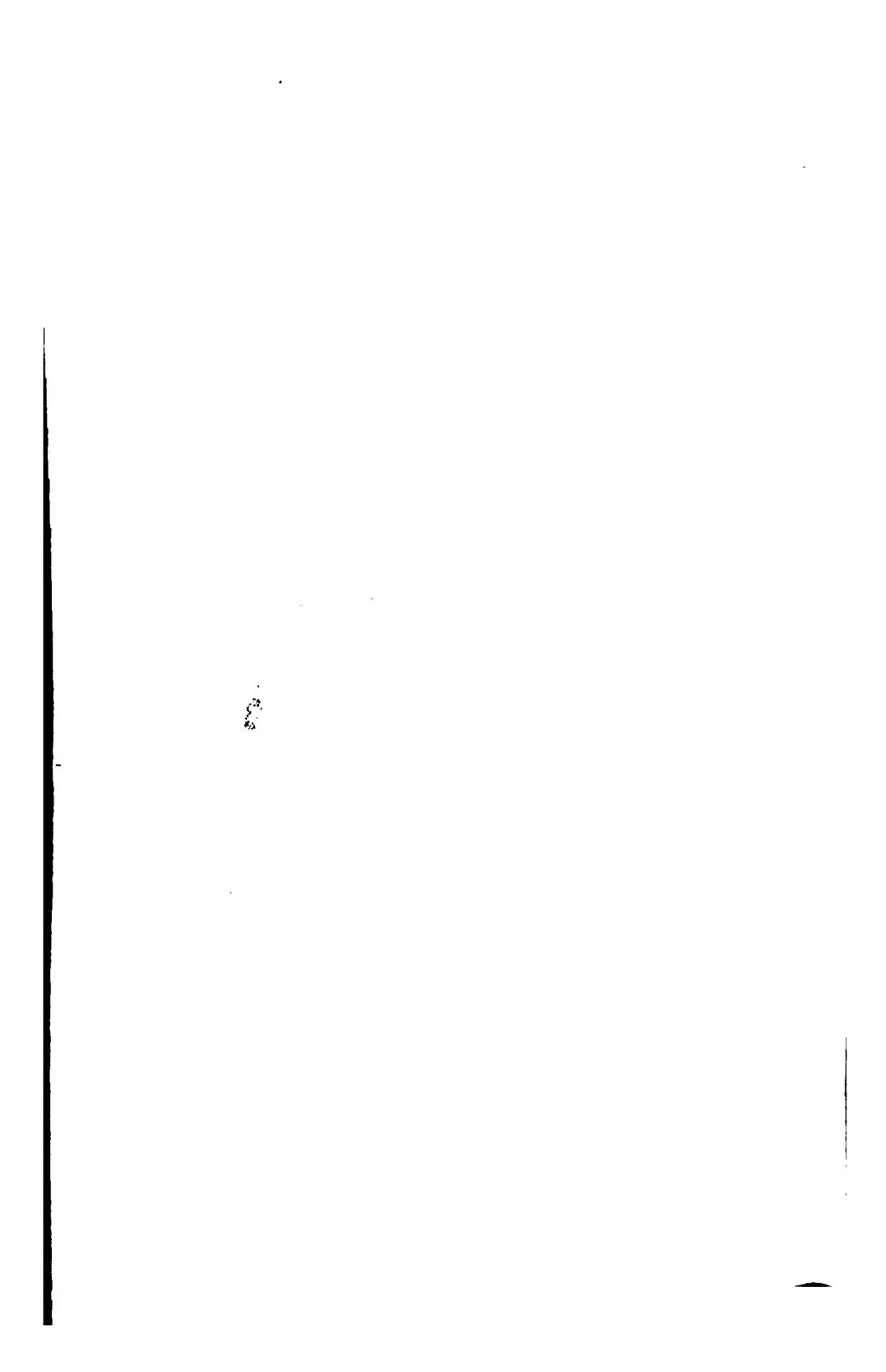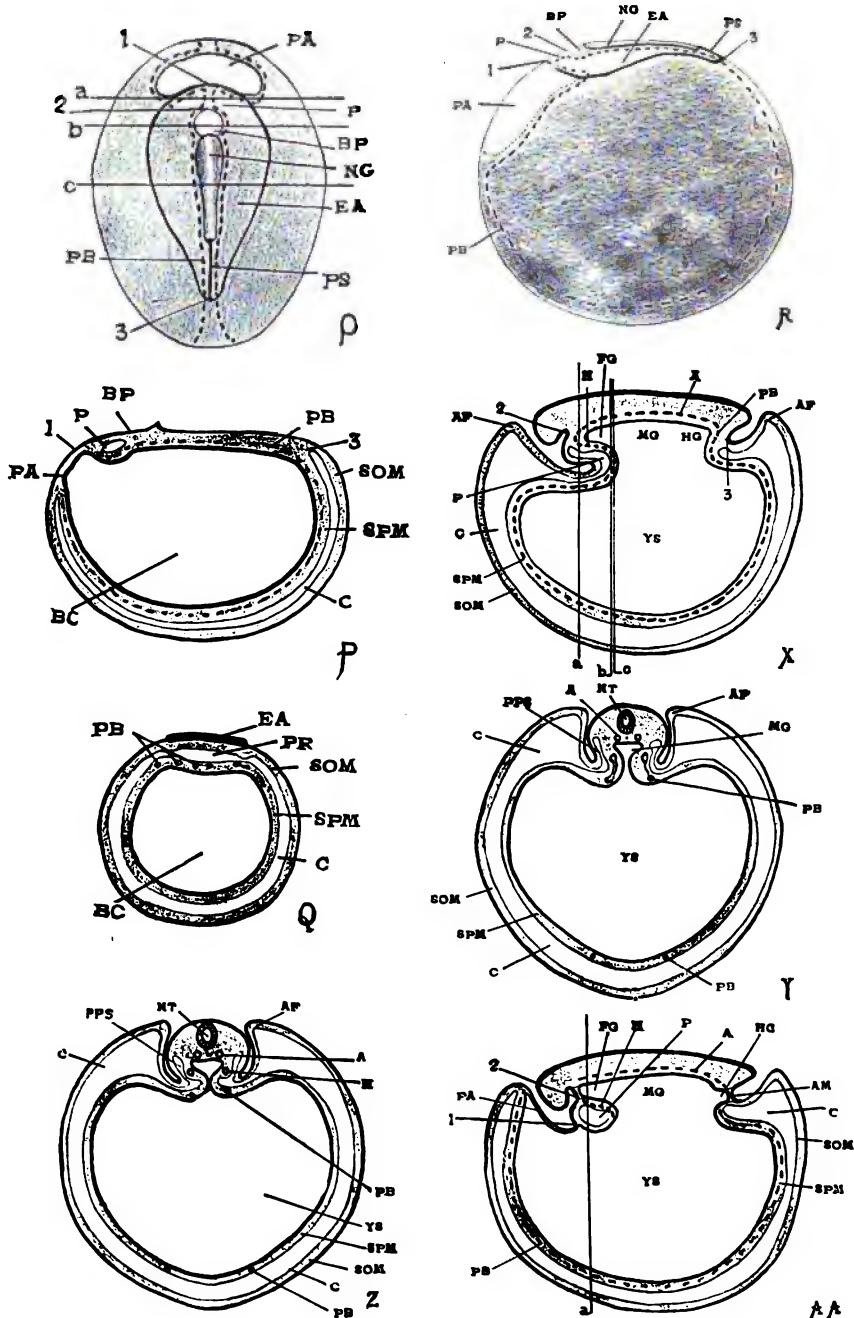
[PLATE I.

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[PLATE II.
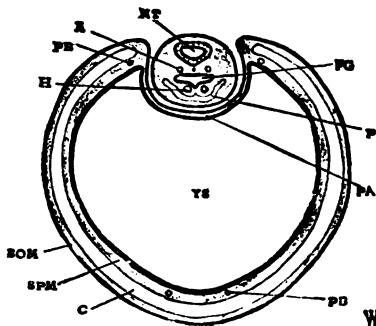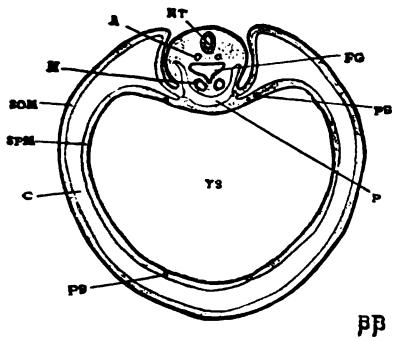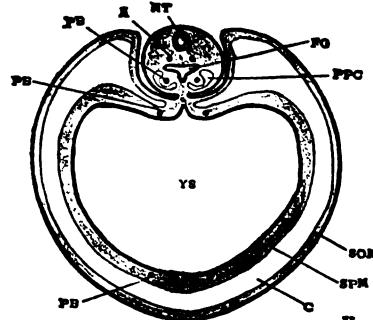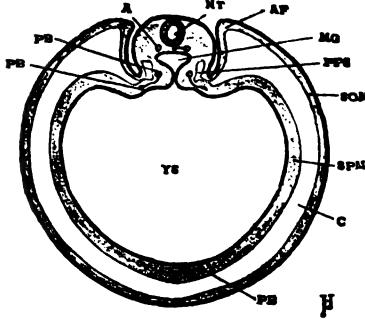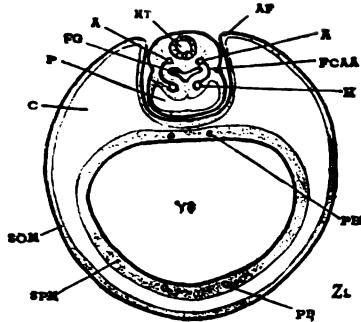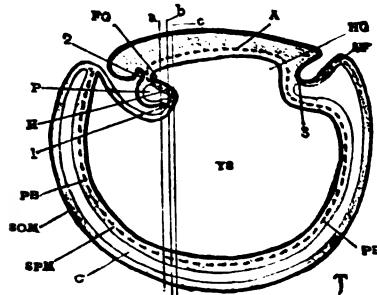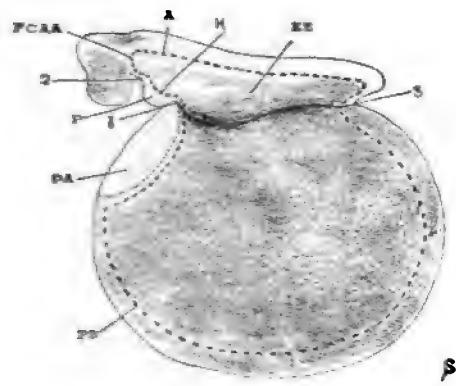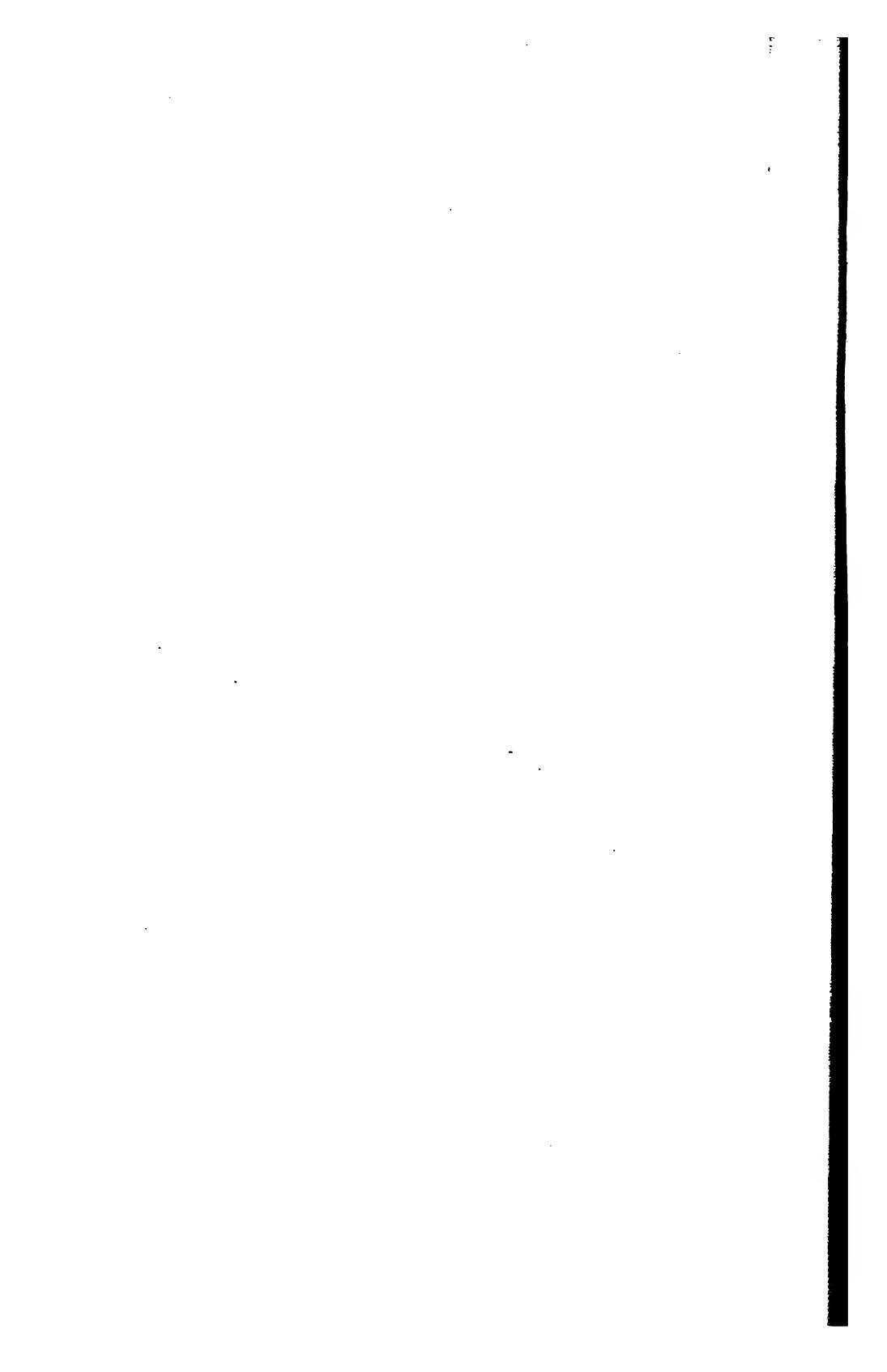
between the pericardial mesoderm and the pericardial cœlom, and the extra-embryonic cœlom immediately in front.

(Y), (Z), and (Z)$_1$—diagrams of transverse sections through the imaginary ovum shown in fig. X, along the lines c, b, and a respectively in fig. X.

(AA)—diagram of a lateral longitudinal section of a ferret's ovum, showing the position of the pericardium after the formation of the head fold ; it also shows that for a time it is bounded below by the yolk sac.

(BB)—diagram of a transverse section of a ferret's ovum along the line a in fig. AA.

EXPLANATION OF FIGURES.

A, aorta.	N, notochord.
AF, amnion fold.	NG, neural groove.
AN, anal membrane.	NT, neural tube.
BC, blastodermic cavity.	MG, midgut.
BP, bucco-pharyngeal membrane.	P, pericardium.
C, cœlom.	PA, proamniotic area.
CM, cardiac mesentery.	PB, primitive blood-vessel.
E, ectoderm.	PPC, pleuro-pericardial canal.
EA, embryonic area.	PPS, pleuro-peritoneal space.
EC, enteric cavity.	PR, pericardial region.
EE, embryo.	PS, primitive streak.
EN, entoderm.	SC, segmentation cavity.
FCAA, first cephalic aortic arch.	SOM, somatic mesoderm.
FG, foregut.	SPM, splanchnic mesoderm.
H, heart.	ST, stomatodeum.
HC, hindgut.	YS, yolk sac.

THE EXTENT TO WHICH THE POSTERIOR SEGMENTS OF THE BODY HAVE BEEN TRANSMUTED AND SUPPRESSED IN THE EVOLUTION OF MAN AND ALLIED PRIMATES. By ARTHUR KEITH, M.D., F.R.C.S., *Lecturer on Anatomy, London Hospital Medical College.*

IN this paper the author proposes to deal with a section of a mass of evidence he has collected for a more accurate determination of the inter-relationships of the anthropoids, and of the kinship of man to that group of Primates. The data given here deal with the suppression of caudal segments, the transmutation of sacral to caudal, lumbar to sacral, and dorsal to lumbar segments, which have occurred in the bodies of that group of Primates of which man and the anthropoids are the living representatives. The evidence is sufficient to show that in the process of the evolution of this group of animals there has been no addition or suppression of segments in either the dorsal, lumbar, or sacral regions of the body; it is only at the distal end of the caudal series that suppression or addition may take place. Further, it will be shown that the transmutation of a body segment, in the evolution of a species, takes place, not by a bound, but by the gradual addition of minute variations.

That the bearing of the evidence of this section on the problem of the origin of the Higher Primates may be quickly grasped, it is necessary to state the working hypothesis which appears to be justified by the whole evidence at the disposal of the author. In the first place, he regards the Primates as divided into two very distinct groups—those which carry the axis of the body in a horizontal position—the *Pronograde Primates*, including the cynomorphous apes of the Eastern and Western hemispheres; and those which carry the axis of the body in an upright position—the *Orthograde Primates*, into which group fall the gibbon,

orang, chimpanzee, gorilla, and man.* The pronograde primate is certainly the earlier type; from it the orthograde was evolved, probably near the commencement of the Miocene Period. The earliest type of the orthograde primate of which we have any knowledge is the gibbon; from the Hylobatian (gibbon) type of orthograde primate have sprung what may be named—for temporary purposes—the *giant primates*, of which type the orang, the chimpanzee, gorilla, and man are the present-day representatives. This type was certainly gigantic, compared to its predecessors. The earliest giant-form we know is Dryopithecus, a Miocene anthropoid.

It will be thus seen that three well marked stages are recognised in the evolution of the highest primates—the pronograde stage, the orthograde stage, and finally, the giant stage. In the evolution of the human stock from that of the arboreal giant primates, a fourth stage must be recognised whereby man, by what means we know not, became adapted to plantigrade progression. The process of transmutation of the pre-sacral segments and suppression of the caudal began with the change from the horizontal to the upright posture during the evolution of the orthograde type from the pronograde. In all present-day pronograde apes—and we may safely suppose the same to hold true of their Miocene ancestry—the segmental formula is nearly constant—26 pre-sacral, 3 sacral, and 6-50 caudal segments. In the gibbon there are 25 pre-sacral segments; in man, the gorilla, and chimpanzee, 24; and in the orang, 23. Evidently, on the assumption of the upright posture there was an abbreviation of the trunk by one segment, and in the evolution of the giant primates still another segment was cut off from the pre-sacral series.

1. *The total number of Segments as determined by the number of vertebræ.*—The first point which required investigation was the total number of segments found in the various genera of living

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* It is now generally recognised that the anthropoids, in their *natural habitat*, carry their bodies in an upright position, *i.e.* are orthograde. The misconception of the older naturalists sprang from their regarding the anthropoids as ground-walkers; for this method of progression they are as little adapted as seals or sea-lions. Instead of the terms *pronograde* and *orthograde*, my friend Mr P. Duncan, now Financial Secretary of the Transvaal, suggested Pronorachitial and Orthorachitial, but I have not used the terms.

Higher Primates, in order that data might be obtained to give a clue to the number of posterior segments which had been suppressed. The number of vertebræ was accepted as an index of the number of segments. In the following table (Table I.*) are given the results of this investigation.

TABLE I.

	Specimens.	Total Number of Vertebræ.								Average.
		29.	30.	31.	32.	33.	34.	35.	36.	
		Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	
Orang . .	30	3·5	20	60	16·5	...	...	...	...	30·8
Gorilla . .	15	6·4	20	33	26·4	13·2	...	...	...	31·2
Chimpanzee	31	9·5	88·4	19	22	6·4	3·2	...	...	31·5
Man . . . (Paterson)	36	...	...	...	5·5	72·2	20	2·7	...	33·3
Man . . . (Bardeen)	104	...	...	...	5·8	85·5	8·5	...	...	33
Gibbon . .	51	...	...	14	32	24	12	12	6	33
Macacus,	...	...	...	...	...	...	...	...	...	33–49
Cynocephalus	...	...	...	...	...	...	...	...	...	36–44
Semnopithecus	...	...	...	...	...	...	...	...	...	58–60
Ateles	...	...	...	...	...	...	...	...	...	60–62
Cebus	...	...	...	...	...	...	...	...	...	54

From Table I. it will be seen (1) that within each genus of the orthograde primates there is a high degree of individual variation: orangs are found with only 29 vertebræ and gibbons occur with 36; between those extremes the vertebral formulæ of the gorilla, chimpanzee, and man form intermediate series; (2) that the process of suppression has affected the segments of the orang most and the gibbon least; (3) man has retained a larger number than any of the other giant primates, because, with the assumption of plantigrade progression, the caudal vertebræ assumed a new rôle in supporting the perineum. The extent of individual variation is evidence of the instability of the structure of the Higher Primates.

* The data of this and the following tables have been obtained from three sources —(1) from publications by many authors; (2) from personal dissections; (3) from the material in the museums of London. A full list of papers dealing with the Anatomy of the Primates was published by the author in 1896 (see "An Introduction to the Study of the Anthropoid Apes," *Natural Science*, 1896; also published separately). A list of subsequent literature from which data have been obtained is given at the end of this article.

The number of segments in a typical pronograde ape, such as the American Cebus or Asiatic Semnopithecus, is from 54 to 60 segments. The primitive orthograde stock arose probably from a pronograde ancestry with a corresponding number of segments; but, arguing from the condition seen in the genera Macacus and Cynocephalus, it is very possible that the caudal vertebræ were already largely suppressed before the orthograde posture was assumed. At least, the presence of a tail is incompatible with the orthograde posture. The number of vertebral segments in the *primitive orthograde stock* was probably about 36, the largest number that occurs in the gibbon—the nearest living representative of that stock.

With the assumption of the upright posture, the flexor and depressor muscles of the tail become modified to form a muscular pelvic floor. The tail of pronograde apes, even when only the four or five basal vertebræ remain, plays the part of a perineal shutter. The caudal vertebræ are amorphous and practically functionless in orthograde apes.

2. *The total number of Segmental Nerves, compared with the total number of vertebræ.*

A forward transmutation of a vertebra is usually accompanied by a corresponding transformation of every element of the body segment to which it belongs. The last lumbar vertebra, for instance, may take on, partly or wholly, the characters of a first sacral; the nerves, the arteries, the muscles of that segment usually undergo a corresponding movement to a corresponding extent. This correlation does not hold good for all the individual variations found in the human body, but it does hold true for the majority of such instances, as may be seen from the observations of Bardeen. When, however, different genera of primates are dealt with, a very close correlationship will be found between all the elements of a body segment. This will be seen in the correlation between the total number of vertebræ and spinal nerves in the various members of the Higher Primates (see Table II.).

[TABLE.

TABLE II.

	Orang.	Gorilla.	Chimp.	Man.	Gibbon.	Prono-grade Apes.
The average number of vertebræ, . .	30·8	31·2	31·5	33·3	33	55
The average number of spinal nerves, .	28	29	30	31	31	33

In the evolution of the orthograde primates, the segmental nerves have undergone a forward transmutation nearly equal to
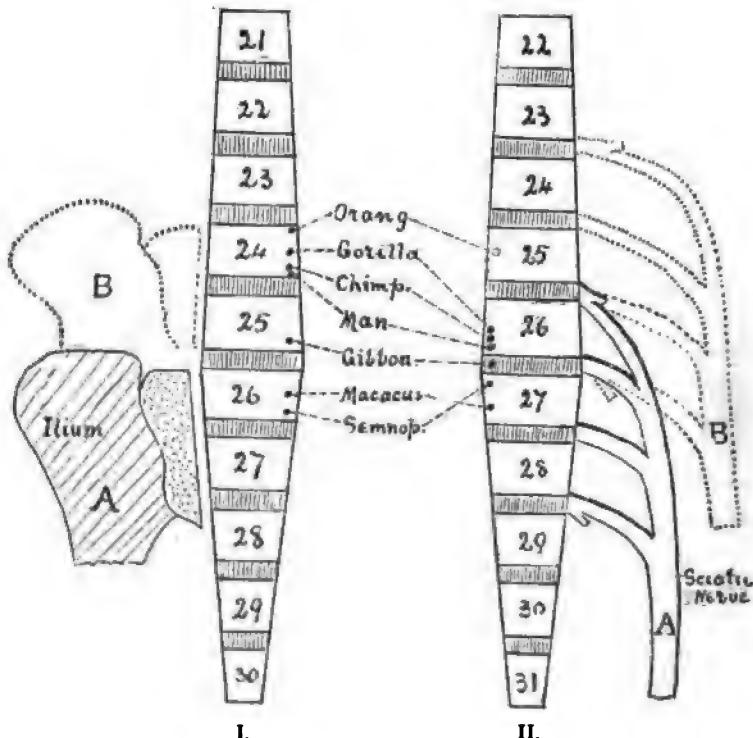
FIG. 1.—Diagram to show (I.) the point in the vertebral column at which sacralisation of the vertebræ commences in various genera of the Higher Primates, and (II.) the central point of emergence of the great sciatic nerve in the same genera.

that of the *body* segments (see fig. 3). On the other hand, sup-

pression of caudal vertebræ has little influence on the total number of nerves; pronograde forms have only two or three pairs more than the gibbon, the most primitive of the orthograde primates. In Ateles, owing to the specialisation of its tail as an organ of prehension, 40 of the segments may carry spinal nerves, but in the more common pronograde apes the number varies from 32 to 34.

3. *The number of Pre-sacral Segments.*—A certain number of body segments are modified to give attachment to the limbs. In pronograde apes the sacral segments are almost constant in number and position, the vertebra of the 27th segment forming the first sacral. With the assumption of the orthograde posture and the shortening of the loins entailed by that change (see fig. 4) there was evidently a transmutation forwards of a whole segment, the last lumbar (26th) becoming wholly sacral in character. The vertebra of the 26th segment became the first sacral. At least in the gibbon, which may be accepted as a representative of the primitive orthograde stock, seeing how closely the present-day animal resembles its Miocene ancestor, the 26th vertebra forms the first sacral. In the evolution of the giant primates there was still a further transmutation forward of one segment, the 25th becoming the 1st sacral. In the orang, for reasons which will be given later, the transmutation has reached the furthest point forward, sacralisation commencing at the proximal border of the 24th segment. The data on which these inferences are founded is given in Table III. In that table it will be seen that the point at which sacral transformation occurs in the segmental series is variable in each genus of the orthograde primates. The genera dealt with in Table III. show sacral transformation setting at every segment between the 23rd and 28th, the variations of one genus overlapping those of the next.

TABLE III.

		Vertebra forming the 1st sacral.						
		23rd.	24th.	25th.	26th.	27th.	28th.	
		Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average
Orang . . .	45 specimens.	5·4	77	17·5	...	...	...	23·1
Gorilla . . .	27 ,,	7·4	37	55·6	...	...	...	23·5
Chimpanzee .	38 ,,	2·6	19·7	55·2	22·3	...	...	23·9
Men	358* ,,	...	3	92	5	...	...	24·02
,, ...	104† ,,	...	5·5	85	7·5	...	...	23·9
Gibbon . .	59 ,,	...	...	15·2	78	6·8	...	24·9
Ateles . . .	6 ,,	...	...	10	80	10	...	25
Macacus . .	19 ,,	...	...	...	45	53	2·8	25·6
Cynocephalus .	8 ,,	...	...	...	37·5	50	12	25·7
Semnopithecus	15 ,,	...	...	...	4	96	...	25·9
Cebus . . .	10 ,,	...	...	...	10	50	40	26·3

For the purpose of comparing the extent to which the hinder lumbar segments have been affected by the process of sacral transformation in each genus, it is necessary to take the average point in the segment-series at which sacral transformation commences. That point can be determined only to an approximate degree. In the orang the point at which sacral transformation commences in the average animal is a little below the proximal border of the 24th segment (see fig. 1, A); sacralisation begins nearly half a segment further back in the average gorilla; in the chimpanzee and man the change commences near the distal border of the same segment. In the negro, sacralisation commences nearly one-third of a segment further back than in white races. In the gibbon, sacral transformation begins near the distal border of the 25th segment, rather more than a segment further back than in the giant primates. In Semnopithecus, probably the best representative now living of the early Miocene pronograde apes, sacral modification starts near the distal border of the 27th segment—one segment further back than in the gibbon.

Why should there have been a forward sacral transmutation

* These statistics are obtained from various authors, including Paterson, Rosenberg, Tenchini, and Papillaut.

† Bardeen's statistics. More than half of his observations were made on negroes in whom the limbs are attached rather more than a third of a segment more posteriorly than in white men.

FIG. 2.—Diagram of a Gibbon (*Hylobates lar*), suspended by its arm to show the adaptation of the muscles and trunk to its brachiating mode of progression —(from a photograph).

of the body segments in the evolution of the orthograde and giant primates? The reason is to be sought for in their adaptation to a new form of locomotion. The long rod-like lumbar region of the jumping and climbing pronograde ape becomes unnecessary for an orthograde form like the gibbon, supported more from its arms than on its legs (see fig. 2). In the evolution of the giant primates the pelvis became still more closely knitted to the body, and the lumbar region correspondingly shortened (fig. 4). On the evidence at present at his disposal, the author believes that the evolution of the primitive orthograde primates early in the Miocene Period was attended by the addition of a lumbar segment to the sacral region; with the evolution of the giant primates later in the Miocene, still another lumbar segment was added to the sacral. It was probably at the stage just mentioned at which the human stock broke away from the common giant primate stock. The assumption of plantigrade progression necessitated a longer loin (fig. 4), which was evidently obtained by a suppression of one pair, perhaps two, of ribs. The transformation of a third lumbar to a sacral segment in the orang is probably a comparatively late acquisition following on its brachiating habits of progression. While the upper extremities of the orang are enormously developed, the lower limbs are comparatively small and show many traits of degeneration. The upper half of its body is developed at the expense of the lower half.

4. *A forward progression in the origin of the great Sciatic Nerve.*—With the transmutation of the distal lumbar vertebræ into sacral there was a movement forward, although not to a corresponding extent, of the points at which the nerve fibres which form the great sciatic nerve make their exit (fig. 1 B). The segmental nerves which contribute to the formation of the great sciatic nerves in various genera of primates are shown in Table IV.

TABLE IV.

Spinal Nerves . Specimens.	23rd.	24th.	25th.	26th.	27th.	28th.	29th.	Central Point of Origin.
Orang . . . 5	5	5	5	5	...	...	...	24·5
Gorillas . . . 5	...	4	5	5	5	1	...	25·7
Chimpanzees . 6	...	4	6	6	6	2	...	25·8
Man (Eisler) 126	2	107	126	126	124	22	...	25·6
,, (Bardeen) 246	11	223	246	246	245	157	35	25·9
Gibbon . . . 9	...	4	9	9	9	5	...	26·
Macacus . . . 10	...	...	5	10	10	10	...	26·7
Semnopithecus . 18	...	...	13	18	18	3	...	26·2

In order to compare one genus with another, and the degree of nerve and vertebral migration, it is necessary to fix a point which marks the centre at which the nerve fibres contributing to the great sciatic make their exit.   In the orang, in which the sciatic nerve arises from the 23rd to the 26th, the central point of its origin lies near the mid point of the 25th segment (see fig. 1 B) ; the central points of exit for the gorilla, chimpanzee, and man lie on the 26th vertebra, in order from above downwards; on the proximal border of the 27th in the gibbon.   Eisler's statistics place the central point for man above those of the gorilla and chimpanzee ; Bardeen's below them, probably because his observations were made on the negro as well as the white man.   The central points of origin of the sciatic nerve in Macacus and Semnopithecus, as shown in fig. 1 B, are situated on the 28th segment.

The observations which have been made on the anthropoids are too limited in number to afford more than a rough approximation to the truth; but it is evident, considering the Higher Primates as a group, that a transmutation of the nerve elements of a segment has accompanied the sacralisation of the vertebræ (compare fig. 1 A and fig. 1 B).   In pronograde apes the central point of origin of the great sciatic nerve and the point at which sacralisation of the vertebræ commences is situated in the 27th segment ; in the gibbon these two points are situated a segment further forwards ; but in the giant primates, sacralisation of the vertebræ starts a segment further forwards than the central point of origin of the sciatic nerve.

It will be seen afterwards that the development of the costal

series influences the position of the origin of the sciatic nerve ; in Semnopithecus and the orang, in which the origin of the sciatic nerve is more proximal than one would expect, the costal series have been abbreviated; in the gorilla and chimpanzee, the costal series reach their full number, and in these animals the central point of origin of the great sciatic nerve is more distal than one would expect. In man, the origin of the great sciatic nerve is also lower than is to be expected, and yet in him the costal series has been reduced, and therefore, if the explanation offered for the others is right, in him the origin of the sciatic nerve ought to be high. The low position in man is probably owing to the great development of his lower extremities.

It is evident that if such a transmutation of the hinder segments of the body has taken place during the evolution of the giant primates, that the segmental distribution of the cutaneous nerves on the lower limbs must have been disturbed. In pronograde apes, as we know from the classical researches of Sherrington, the segmental distribution of the cutaneous nerves is regular and symmetrical in the lower limbs, but such symmetry and order have not been found in the segmental distribution of the nerves in the lower limbs of man. The discrepancy is probably due to a disturbance which occurred in the forward transmutation dealt with here. It is probable that the segmental distribution of cutaneous nerves is not exactly alike in the lower limbs of any two human bodies, and hence the discrepancy in the results of different observers.

5. *The number of Sacral Segments.*—Since it is the 27th, 28th and 29th body segments which undergo sacral modifications in the typical pronograde apes of the Western and Eastern hemispheres, there can be little doubt that these were the sacral segments in the pronograde stock from which the orthograde was evolved. With the assumption of the upright posture in the early orthograde primates, of which the gibbon is the best living representative, the 26th segment underwent sacral modifications ; with the evolution of the giant primates, still another, the 25th, was added to the sacral segments ; and still later, in the stock of the orang, the 24th. Thus in the orang there ought to be found six sacral vertebræ; in the gorilla, chimpanzee, and man five, in the gibbon four, in pronograde apes three.

The annexed table (Table V.) will show how far this expectation is well founded.

TABLE V.

Number of Sacral Vertebræ.	2.	3.	4.	5.	6.	7.	8.	Average.
Specimens.								
Orang . . . 37	...	...	12	24	1	...	...	4·7
Gorilla . . . 24	...	8	1	13	5	1	1	5·1
Chimpanzee . 31	...	2	3	13	12	1	...	5·2
Man (Paterson) 100	...	...	2·6	61·8	34·3	1·13	...	5·3
,, (Bardeen) 100	...	...	5·7	86·6	7·7	...	...	5·02
Gibbon . . . 68	...	12	26	26	4	...	...	4·3
Ateles 3	...	1	2	...	...	...	...	3·6
Semnopithecus	rare	com.	...	...	...	...	...	– 3
Macacus	...	com.	rare	...	...	...	...	+ 3

On the average, the number of sacral vertebræ answers to the number expected. In the gibbon there are 4, in man, the gorilla and chimpanzee 5, but in the orang there are less than 5, while 6 is the number to be expected. The reduction in the number of the sacral vertebræ in the orang is due, as will be shown in the next paragraph, to a caudal transformation of the posterior sacral segments. In pronograde apes only two vertebræ articulate with the ilium, in orthograde there are three. The gibbon, gorilla and chimpanzee show a greater instability in the number of sacral vertebræ than man, because in them it plays a less defined and less important part in their locomotion.

6. *The caudal transmutation of the distal Sacral Vertebræ.*— While the distal lumbar segments were undergoing a sacral transformation, there was only a slight movement in the direction of turning distal sacral segments into caudal. In man and the gibbon the first caudal vertebræ is the 30th, and this seems to be the primitive form, for in all the typical pronograde apes the 30th is the first vertebra of the tail. In the orang and gorilla, in which the forward transmutation of segments is most marked, the last sacral (29th segment) has undergone a caudal modification. As may be seen from Table VI., in which the serial number of the vertebra forming the first caudal or coccygeal is given, the extent of individual variation is very great.

TABLE VI.

Vertebra forming the first caudal.	27th.	28th.	29th.	30th.	31st.	32nd.	
Specimens.							Average.
Orang 15	...	3	10	2	...	...	− 29
Gorilla . . . 18	2	4	4	7	1	...	+29
Chimpanzee . . 31	2	8	3	15	3	...	29·3
Man (Paterson). 132	...	...	3	103	24	2	30·2
,, (Bardeen) . 104	...	...	6	89	9	...	30
Gibbon . . . 49	...	...	12	19	12	6	30·2

Occasionally in Macacus the 29th, and in Semnopithecus and Cebus the 31st vertebra forms the first caudal; but normally in all three genera, the 30th forms the first of the caudal series.

7. *The number of Caudal or Coccygeal Vertebræ.*—The distal sacral and all the caudal vertebræ of the anthropoids are frequently so vestigial in form that it is hard to say which is the first caudal, and how many the caudal vertebræ are in number. It is probably owing to this difficulty that there is a discrepancy in the statistics which are given relating to the orang. In that anthropoid the 24th is the first sacral vertebra; there were, on an average, less than 5 sacral vertebræ; therefore the first caudal ought to be the 28th and not 29th, as the statistics show. Table VI., too, is founded on a smaller number of animals than Tables III. and V. In the following table (Table VII.) the number of caudal vertebræ in each genus is given.

TABLE VII.

Number of Caudal Vertebræ.	2.	3.	4.	5.	6.	7.	
Specimens.							Average.
Orang . . . 20	4	12	2	2	...	...	3·1
Gorilla . . . 13	3	5	3	2	...	...	3·3
Chimpanzee . 32	5	12	5	7	3	...	3·7
Man 104	9	95		...	...	...	3· (?)
Gibbon . . . 54	6	18	22	5	1	2	3·7
Semnopithecus ...	...	...	...	...	...	...	30
Macacus	...	...	...	...	...	...	4–21
Cynocephalus	...	...	...	...	...	...	6–10

The most striking point relating to the caudal vertebræ of the anthropoids is their variability in number, and their amorphous

and vestigial character. In comparison with these, the human caudal vertebræ are steadfast in number and much better formed.

With the assumption of the upright posture in the primitive orthograde primates, the tail became a useless structure and underwent suppression. It was no longer required to play the part of a balancing rod or perineal shutter. It is not improbable that the process of caudal retrogression had set in long before the change in posture took place, for in many modern species of pronograde apes belonging to the Macaque and baboon genera, the typical number (30) of caudal segments is reduced to 4 or 6, but in such cases of reduction the vertebræ still retain all the characters of fully developed caudal vertebræ, still act as a perineal shutter, and in no way resemble the amorphous remnants of the caudal vertebræ in orthograde primates. With the change of posture there was a radical change in the formation of the pelvic floor.

The adaptation of the tail as a prehensile organ, which has led to many changes in the structure of South American apes, is probably to be regarded as a comparatively recent acquisition.

8. *The transmutation of Lumbar Segments as indicated by the origin of the anterior crural nerve.*—In the segmental origin of the anterior crural or femoral nerve, evidence is to be found of the degree to which the proximal lumbar segments have been affected in the general forward transmutation that set in with the assumption of the upright posture. The segmental nerves which contribute to the formation of the anterior crural in various groups of the Higher Primates is set forth in Table VIII.

TABLE VIII.

	Specimens	20. Per ct.	21. Per ct.	22. Per ct.	23. Per ct.	24. Per ct.	25. Per ct.	26. Per ct.	Central Point of Origin.
Orang	9	1	7	9	9	1	...	...	22
Gorilla	6	...	1	5	6	6	1	...	23
Chimpanzee	11	...	3	9	11	10	2	...	23
Man (Bardeen)	246	2	90	246	246	246	37	...	22·8
Gibbon	11	...	...	1	10	11	6	...	23·8
Semnopithecus	10	...	...	3	6	10	7	...	23·8
Macacus	9	...	...	...	5	9	9	...	24·1

In fig. 3 is shown the central point of origin of the anterior crural nerve in each genus of the Higher Primates dealt with here, and it will be seen by comparing the origin of this nerve with that of the great sciatic that there is not a close correlation between the forward movements of those two nerves. The condition in Semnopithecus may be taken as typical of pronograde apes, and in it the central point of origin of the anterior crural nerve is situated near the distal border of the 24th vertebra. In the orang the origin of this nerve has moved forwards nearly two segments; in man, the gorilla and chimpanzee, one segment; but in the gibbon the pronograde origin is retained. It will be seen presently that the origin of the anterior crural nerve is correlated with the development of the costal series; with the retrogression of the distal ribs there is a forward movement in the origin of this nerve. The origin of the anterior crural is acted on by two influences: (1) the forward transmutation of lumbar to sacral segments, and (2) of the transformation of dorsal to lumbar.

9. *The origin of the Obturator Nerve.*—In the transmutation of lumbar segments the obturator nerve does not follow closely the migration of the anterior crural. In Table IX. are shown the various segmental nerves which contribute to the formation of the obturator.

TABLE IX.

	Specimens.				Spinal Nerves.						Central Point of Origin.
					21. Per ct.	22. Per ct.	23. Per ct.	24. Per ct.	25. Per ct.	26. Per ct.	
Orang .	. 8	.	.	.	2	7	8	...	...	...	22·3
Gorilla	. 6	.	.	.	...	5	6	6	1	...	23·2
Chimpanzee .	. 4	.	.	.	1	3	4	3	...	...	22·8
Man .	. 246	(Bardeen)	.	84	246	246	245	25	...	22·8
Gibbon	. 11	.	.	.	...	...	4	11	7	...	24·2
Semnopithecus	9	.	.	.	...	...	...	9	9	1	24·6
Macacus	. 8	.	.	.	...	...	1	7	8	4	24·7

In man the origin of the anterior crural nerve and obturator is practically the same, the central point of origin for both being the junction of the distal fifth with the proximal four-fifths of the 23rd vertebra. In pronograde apes, on the other hand, the

obturator nerve takes its origin at least half a vertebra behind
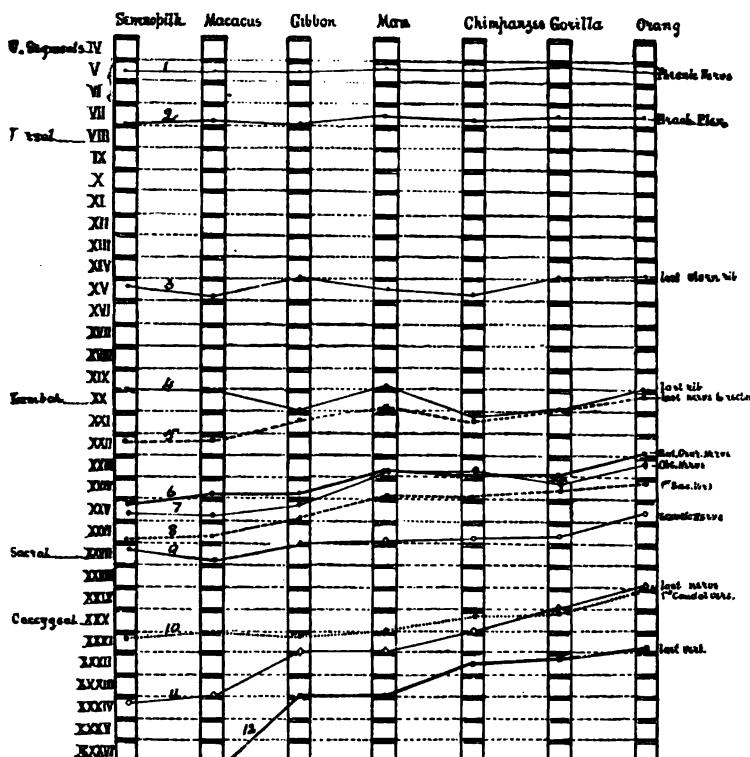
Fig. 3.—A composite diagram representing the vertebral columns, from the 4th to the 36th vertebræ, of various genera of Higher Primates.   On each vertebral column, founded on the statistics given in the text, are represented the following points :—

(1) The central point of origin of the phrenic nerve.
(2)　　　 ,,　　　 ,,　　　 ,,　　　　brachial plexus.
(3) The segment carrying the last sternal rib.
(4)　　　　 ,,　　　 ,,　　　 ,,　　 rib.
(5) The point of origin of last nerve to rectus abdominis.
(6) The central point of origin of the anterior crural or femoral nerve
(7) The central point of origin of the obturator nerve.
(8) The point at which sacralisation of the vertebræ commences.
(9) The central point of origin of the great sciatic nerve.
(10) The point at which the vertebræ becomes caudal.
(11) The point of origin of last spinal nerve.
(12) The last vertebra.

that of the anterior crural ; in the gibbon, orang and gorilla the

origin of the obturator approaches, in the order named, the origin of the anterior crural; in the chimpanzee, the origin of the obturator appears to be slightly proximal to that of the anterior crural.

10. *The number of Rib-bearing Segments.*—Owing to the lack of evidence, it is a difficult matter to fix approximately the number of rib-bearing segments in the primitive stock of the orthograde primates. Even in typical living pronograde apes such as Semnopithecus and Colobus, there has been a suppression of at least one pair of ribs in the more recent periods of their evolution, so that in the matter of rib-bearing segments these no longer represent the pronograde stock which gave rise to the orthograde. From the evidence adduced in Table X., in which the last rib-bearing segment is given in most of the genera of the Higher Primates, it will be seen that the 8th to the 21st segments are costal-bearing, making 13 pairs of ribs.

TABLE X.

	Specimens.				Last Costal-bearing Segment.						
					17.	18.	19.	20.	21.	22.	
				Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average.
Orang .	. 31	.	.	...	4	87	9	...	...		19·02
Man .	. 104 (Bardeen)		...			5·7	90*	3·8	...	...	18·9
Gorilla .	. 29	.	.	...	...	10	84	6	...		19·96
Chimpanzee .	35	.	.	...	...	...	83	17	...		20·1
Gibbon .	. 33	.	.	...	...	9	82	9	...		20
Semnopithecus	31	.	.	...	3	94	3	...	...		19
Macacus	. ...	.	.	...	...	95	5	...	...		19·05
Cynocephalus	...	.	.	...	...	25	75	...	...		19·7
Ateles .	. ...	.	.	...	...	...	...	100	...		21

Assuming that the 20th was the last costal-bearing segment in the primitive stock from which the various genera of primates dealt with here arose, it will be seen that this number has been approximately retained in the gorilla, chimpanzee and gibbon. In the pronograde apes of the Eastern hemisphere the number has been reduced, Cynocephalus suffering the least degree

* In 40 per cent. of these the 12th rib was less than two inches long, and therefore could scarcely be regarded as forming part of the thorax.

of suppression. It is probable that the number has been increased in Ateles, and there appears to be a tendency to increase in the chimpanzee. The fact that the diaphragm in all the genera of primates mentioned in the above tables has an attachment to the rib or costal process of the 20th segment, however vestigial that process may be, points to the fact that the 20th segment has always been, as far as the Higher Primates are concerned, the last of the respiratory segments.

It will be observed, too, that there is only a slight correlation between the forward progression of the sacral segments and the reduction of the distal costal processes. The orang, in which three lumbar have become sacral segments, has suffered reduction in only one costal segment. The reduction in the number of the costal segments in man, Semnopithecus and Macacus is due, not to any retrogression in their respiratory system, but to an elongation of the lumbar region of the spine rendered necessary in those forms by their manners of progression.

11. *Reduction in the number of Sternal Segments and Sternal Ribs.*—In the suppression of the distal costal segments there has been some reduction of the distal sternal segments, which may be indicated, as shown in Table XI., by the number of sternal ribs.

TABLE XI.

Last Sternal Rib.	6th.	7th.	8th.	9th.	10th.	
	Per ct.	Per ct.	Per ct.	Per ct.	Per ct.	Average.
Orang	18	82	...	...	...	6·8
Man (white) . .	2	90	8	...	...	7·2
,, (negro) . .	...	70	30	...	...	7·3
Gorilla	5	85	10	...	...	7
Chimpanzee . .	...	54	46	...	...	7·4
Gibbon	8	78	14	...	...	7
Semnopithecus .	4	72	24	...	...	7·2
Macacus	...	12	88	...	...	7·8
Cynocephalus . .	...	...	60	40	...	8·4
Ateles	...	...	33	55	35	9

With some exceptions, the reduction in the number of sternal ribs corresponds in a minor degree with the sacral transmutation of the distal lumbar segments, and also with the reduction in the total number of costal-bearing segments. The sternal ribs

are fewest in the orang, in which the forward sacral transmuta-
tion has proceeded furthest; the gorilla follows next; the chim-
panzee has a larger number of costal-bearing segments and
sternal ribs than any of the other orthograde primates. The
reduction in the number of sternal ribs in the gibbon has to be
sought for in the peculiar development and use of the pectoral
muscles (see fig. 2).

12. *Transmutation in the distal, cervical and proximal dorsal
Segments.*—The proximal 18 segments of the body, compared
with those situated more distally, have undergone a very slight
degree of transmutation during the evolution of the various
genera of primates. In all the extant genera, as was no doubt
the case in the original stock of the primates, the 8th is the
first rib-bearing segment. Occasionally in man, the gibbon and
chimpanzee, the 7th cervical segment may take on partially or
even wholly the characters of the 8th; very rarely indeed is
there a backward transmutation when the 8th takes on the
characters of the 7th. The extent of the transmutation in this
region of the body may be measured by the central points of
origin of (1) the phrenic nerve, (2) the brachial plexus; and
although the data I have collected bearing on the segmental
origin of those two relate to a comparatively small number of
individuals, they are sufficient to show that, in the origin of the
brachial plexus and phrenic nerve, there is not, as shown
in fig. 3, half a segment of difference between the two most
extreme forms. The central point of origin of the phrenic
nerve is always at a point on the proximal half of the 5th
segment, that of the brachial plexus on the distal half of the
7th.

Occasionally, too, there is a partial occipitalisation of the first
(cervical) body segment, the atlas being incompletely separated
from the occipital bone.

13. *The last Segmental Nerve of the belly wall.*—An examina-
tion of the ventral aspect of the body reveals the fact that the
segmental abbreviation of the trunk has proceeded rather more
slowly on the ventral than on the dorsal aspect. The data on
which this statement is based is given in Table XII. There the
last nerve supplying the rectus abdominis is given in groups of
the Higher Primates.

TABLE XII.

Last Segmental Nerve to Rectus.	19th.	20th.	21st.	22nd.	23rd.	
Specimens.						Average.
Orang 5	4	1	...	...	...	19·2
Gorilla 4	2	1	1	...	...	19·7
Man (Bardeen) . 267	44	214	9	...	...	19·8
Chimpanzee . . 7	...	5	2	...	...	20·3
Gibbon 11	...	7	3	1	...	20·4
Semnopithecus . 3	...	...	2	1	...	21·3
Macacus . . . 6	...	...	4	2	...	21·3
Cynocephalus	...	...	...	...	...	22

14. *Abbreviation of other structures.*—In comparing the level at which certain viscera occur in the body, one must remember that most of the anthropoids dissected are young animals, and the position of their viscera is comparable, not with those of adult man, but with those of the child. The point of bifurcation of the trachea, the position of the arch of the aorta, and the level of the cricoid cartilage correspond in man and anthropoid. Alteration in position affects only viscera on a level with the distal lumbar segments. Thus the abdominal aorta bifurcates at the level of the 24th vertebra in pronograde apes, or even at a point situated more distally; at a level with the 23rd vertebra in the gorilla, chimpanzee, gibbon and man; and at the 22nd in the orang.

The spinal cord terminates at the 19th vertebra in the orang, 22nd in the *baby* gorilla, 20th in the chimpanzee, 21st in man, 22nd in the gibbon, 23rd in Macacus and Semnopithecus, and 24th in Ateles.

15. *A comparison of the proportions of the cervical, dorsal and lumbar regions of the spine.*—In fig. 4 are represented diagrammatically the relative lengths of the cervical, dorsal and lumbar regions of the spines in various genera of the Higher Primates. The diagram is founded on measurements made by Cunningham, the author, and other observers on several specimens of each genus. It will be seen at once that with the *sacralisation* of the distal lumbar segments there is also a reduction in the relative length of the lumbar region. In the orang, where the process has proceeded furthest, the lumbar region is shortest, measuring only 24 per cent. of the pre-sacral

part of the spine. The lumbar region is relatively longest in the pronograde apes. Man occupies a curious position. At birth the lumbar region is only 27 per cent. of the pre-sacral spine ; but as the child learns to walk, the lumbar region elongates and becomes ultimately 32 per cent. of the spine, equal to that of the gibbon. Thus at birth the proportions of the regions of the human spine are those of an anthropoid. The short lumbar region of the orang, as already explained—and the explanation is
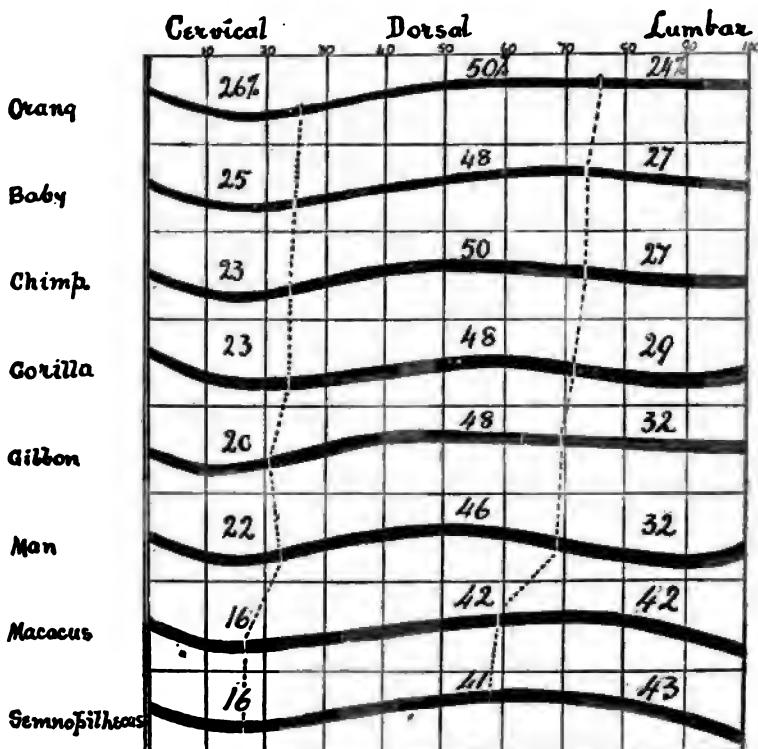
FIG. 4.—Diagram to show the relative proportions of the cervical, dorsal, and lumbar regions of the spinal column of the Higher Primates.

also applicable to the gorilla and chimpanzee—is owing to its brachiating habit of progression. While its arms and the upper half of its trunk are greatly developed, the lower half of the trunk and lower extremities are small and out of proportion.

The cervical and dorsal regions of the spine retain practically

the same relative proportions in all the orthograde primates. The apparent shortness of the neck in pronograde apes is due to the relatively long lumbar region.

SUMMARY.

With the evolution of the orthograde from pronograde primates, the lumbar region becomes relatively shorter, the process of abbreviation being brought about by the transformation of the 26th (lumbar) segment to the 1st sacral; in the evolution of the giant primates (the ancestral stock of man, the gorilla, chimpanzee, orang), the lumbar region was further shortened, the 25th segment becoming gradually sacral in character.   In the origin of the human stock, by the assumption of plantigrade progression, the lumbar region again became elongated, and it is possible that there may be in progress a slight backward migration—a tendency for the 25th to again become lumbar in character; but the fact that the point at which sacralisation commences is situated more distally in the negro than in the white man is against this assumption.   In the evolution of the orang the lumbar region was further shortened, the 24th segment becoming sacral in character. That is the working theory which I put forward to account for the segmental arrangement of vertebræ and nerves in the Higher Primates.

All the data given here support Rosenberg's conception that in comparing two animals, the 19th segment of one corresponds to the 19th of the other, and the 20th to the 20th; that one segment may assume one or all the characters of its neighbour on either side; that suppression or intercalation of segments has played no part in the evolution of the higher mammals.   It is certainly true that unilateral division of a segment occurs; it is possible that the division may be occasionally bilateral, but such a division is comparable to the abnormal process of dichotomy that produces in the embryo a double digit or a twin monster.

The extensive series of specimens in the Warren Museum in Harvard University, described recently by Professor Dwight,

shows how every intermediate form occurs between the sacralisation of the 24th and of the 26th segments, and that it is not a matter of lifting out or inserting a segment, but the gradual transformation of the characters of one segment into those of the one lying next it in the series.

I gladly avail myself of this opportunity of acknowledging my indebtedness to Dr Charles Hose of Sarawak, who, at much personal sacrifice, has sent me an ample supply of primate material.

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SOME CARDIOGRAPHIC TRACINGS FROM THE BASE OF THE HUMAN HEART. By Astley V. Clarke, M.D. Cantab., *Physician to the Leicester Infirmary*, and J. Sholto C. Douglas, *Christ Church, Oxford*.

A WAIF male child, aged about 5, presenting the unusual abnormality of congenital bifurcation of the manubrium sterni,

Photograph showing extent of the fossa.   The lower marks on the skin are the cheloid scars.

has recently been an inmate of the Leicester Infirmary.   Owing to the rarity of this condition, the child is of great interest,

because the beginnings of the great vessels, and probably the base of the heart itself, are available for cardiographic tracings in the human subject.

The child appears to be healthy in every way, the only other abnormality being some cheloid scars situated on the skin covering the depression where the manubrium ought to be.

The adjoining photograph shows the extent of the fossa, but the following measurements were also made :

> Separation of the clavicles $2\frac{1}{4}$ in.
> Length of fossa   .   . $2\frac{2}{5}$ „
> Width of fossa—at top $2\frac{1}{4}$ in.
>   at second rib $1\frac{3}{4}$ in.
> Depth of fossa. $\frac{3}{8}$ in.
> Length of sternum from imaginary top. 4 in.
> Length of median piece, 1 in.
> Sternal width, 1 in.

Pulsation of a strongly marked character, over an area of the size of half-a-crown, is seen in the floor of the fossa during tranquil respiration, but on deep respiration the edges of the lungs become inflated and bulge into the fossa, rendering the pulsation far less visible.

No tumour due to venous stasis appears at any period of the cardiac cycle.

X-ray observations were made to determine, if possible, exactly what portion of the heart was presenting at the fossa, but not with great success. A skiagraph is here produced when the child is lying prone on the plate. and the margins of the depression are outlined with wire, the nipples being indicated by metal pieces.

From this it will be seen that the abnormality does leave some portion of the heart itself uncovered, and this observation confirms the estimation of the position of the heart, as made out by percussion of the deep cardiac dulness. The heart apex beat being situated behind a rib, prevented tracings from being obtained there.

The heart rhythm is normal, as also are the cardiac sounds.

Cardiographic tracings were taken by means of Marey's tambours, both when the child was awake and asleep, the

former being attended with great difficulty owing to the restlessness of youth.

Skiagraph showing relation of heart to the fossa.

The tracings are of interest, since it will be seen that a small but very definite rise of the lever constantly takes place before the great impulse which occurs on the opening of the aortic valves.
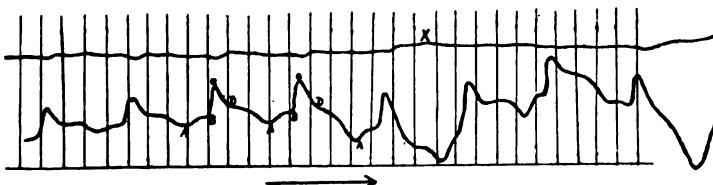
FIG. 1.—To be read from left to right. Each division represents one-tenth of a second.

The upper curve represents a tracing from the axillary artery; the lower being obtained synchronously from the pulsating chest area.

At X the movements of the child caused the bottom of the tambour on the axillary artery to slip off the vessel.

The portion of the curve A to D in fig. 1 gives the duration of systole of the heart, since in our interpretation D is the

dicrotic notch, while the small rise A B is due to that period of
systole which precedes the opening of the aortic valves. This
shorter period occupies about 1.10 sec. (when the child was
awake) to 2/10 sec. (during sleep),—and corresponds with the
well known observations as to the interval between the rise of
the intra-ventricular and intra-aortic pressures made by Chauveau
and Marey upon the horse. (Hürthle, in the dog, found 1/50 to
1/25 sec., but in this animal the heart beats at a faster rate.)

FIG. 2.—To be read from left to right. The time is given in tenths of seconds.
   The curve was obtained from the pulsating chest area while the boy was
   asleep.

Discussing these tracings in more detail, we find from fig. 1
that the whole cycle of events takes from four to five tenths of
a second. The first portion of this time is occupied by a slight
rise of the lever, lettered in fig. 1 A to B, and this takes between
one and two tenths of a second. This initial rise is suddenly
followed by a very sharp ascent, viz., B to C; then follows a
gradual descent from C to A, which is interrupted by a slight
but constant wave D.

In this figure is also recorded a tracing of the axillary artery
taken synchronously (tracings could not be obtained from the
carotids). From a comparison of the two tracings it will be seen
that the rise of the axillary lever occurs immediately after the
summit C of the tracing from the chest, that is, about 1/20 sec.
after the point B. This interval of time would practically
correspond to the delay in the axillary pulse, such as would be
caused by the transmission of the pulse wave from the root of
the aorta to the axillary artery. From this interpretation of the
record the aortic rise of pressure begins at B, and hence the
portion A B of the lower curve (fig. 1) not being due to any rise
of blood-pressure in the aorta, must be caused by events occur-
ring during the systole of the heart. In our judgment it gives
the period elapsing from the commencement of systole to the
opening of the aortic valves. In larger mammals (Horse, etc.)
it has been shown that the time taken during the systole of the

heart in setting up an intra-ventricular pressure sufficient to open the aortic valves is from one to two tenths of a second, and we think that our own observations determine this time in the case of the human heart, since A B is about 1/10 sec. in fig. 1 and 2/10 sec. in fig. 2. The portion of the curve B C A represents the aortic pulse, D being the dicrotic wave; this aortic pulse record in man is of interest, in that it has been obtained when the viscera are in their normal position.

In fig. 2 we give a further tracing which was obtained during
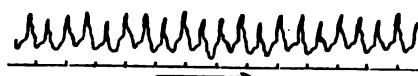
FIG. 3.—To be read from left to right. The time is marked in seconds. This tracing was obtained from the pulsating chest area on a slowly moving drum.

sleep, showing the same phenomena but spread over a slightly longer period.
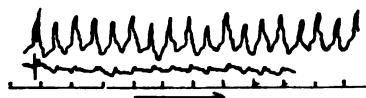
FIG. 4.—To be read from left to right. Time in seconds. Synchronous curves of the pulsating chest area (above) and of the axillary artery (below).

Figs 3 and 4 are records on a more slowly moving drum, the latter showing a tracing of the axillary artery synchronously obtained.

All the tracings are reduced one-half.

In conclusion, we offer our thanks to Professor Gotch of Oxford for his criticism, and also for the loan of the instruments used for obtaining the tracings.

A STUDY OF THE CEREBRAL CORTEX IN A CASE OF CONGENITAL ABSENCE OF THE LEFT UPPER LIMB. By T. G. MOORHEAD, M.B., B.Ch., *Chief Demonstrator of Anatomy, Trinity College, Dublin.* (PLATE III.)

IN the volume of *Brain* for 1878 an account (1) of the cerebral hemispheres of an individual whose left arm had been deficient from birth was published by Sir William Gowers, and in the volume of the same journal for 1880 an account (2) of a similar case was published by Professor Bastian and Victor Horsley. In both of these cases the ascending parietal convolution on the right side was found to be of less extent than that on the left side over an area which closely corresponded with the centres *a*, *b*, *c*, *d* of Ferrier, while in neither of the cases was any inequality of the ascending frontal gyri observed, and indeed in the former of the two it was explicitly stated that these gyri were exactly equal on the two sides. At the time when these papers appeared the views of Ferrier regarding the localisation of arm movements in the cerebral cortex were very generally received, and the appearance of the brains in the cases referred to was held to afford additional evidence in support of the experimental proof that the centre for such movements was placed in the ascending parietal gyrus. However, whilst advancing their case in support of the view " that there is a co-relation of some kind between the functional activities of those regions of the ascending parietal convolution and the movements of the opposite hand and fingers," Bastian and Horsley maintained that such a co-relation might exist even though its commonly received explanation was incorrect, and that before any definite conclusion could be drawn from the examination of such cases more definite information must be obtained regarding asymmetry of the ascending parietal gyri in normally developed persons; and in the light of recent discoveries the words may be regarded as almost prophetic.

Examination of the plates which accompany the two papers shows that in the former of the two specimens there is without doubt an obvious diminution in size of the ascending parietal

gyrus on the right side, almost exactly opposite the arm-centre of Sherrington and Grünbaum (3), but in the latter case the diminution in size appears to lie at a slightly lower level, the gyrus being well developed opposite the arm-centre. In both cases the arm-centre in the frontal gyrus is strongly developed on each side, and the diminution in size of the parietal region is only slightly, I believe, greater than is often met with in the brains of normal persons.

Through the kindness of Professor Cunningham, I have recently had an opportunity of examining the brain of an adult man in whom the distal portion of the left upper limb was congenitally absent. The photograph reproduced in Pl. III. fig. 1, which was taken from a cast, shows the condition of the arm, the five small projections immediately below the elbow joint being the representatives of the undeveloped finger buds.

The two cerebral hemispheres were well developed (Pl. III. fig. 2), and did not present any marked asymmetry in their convolutions and fissures. The following measurements of the transverse extent of the ascending frontal and parietal gyri were obtained.

Right Ascending Frontal.		Left Ascending Frontal.
8·0 mm.		8·0 mm.
12·25 ,,		17·0 ,,
20·0 ,,	Arm-area.	19·0 ,,
9·0 ,,		8·75 ,,
10·75 ,,		16·0 ,,
12·0 ,,		15·0 ,,

Right Ascending Parietal.		Left Ascending Parietal.
7·0 mm.		6·5 mm.
7·75 ,,		7·5 ,,
10·25 ,,	Opposite to	10·0 ,,
7·0 ,,	Arm-area.	10·75 ,,
5·5 ,,		7·25 ,,
11·5 ,,		11·0 ,,

From these measurements it is seen that on the whole the right side of both the ascending frontal and ascending parietal gyri in the region of the arm-centre is smaller than the corresponding area on the left side, the difference being more marked, as a reference to the figure (Pl. III. fig. 2) will show,

in the lower part of the latter convolution. The area was, how-
ever, well developed even on the right side, and in drawing con-
clusions from the above figures the fallacy of measurements of
the superficial extent of small cortical areas, especially in the
neighbourhood of a sulcus so deep as that of Rolando, in which
I have found that on an average twenty-six square centimetres
of cortex lie below the level of the general surface of the brain,
must be borne in mind, and also the possible obscuring influence
of small secondary sulci, which, though they form lines of
demarcation, really increase the extent of the main gyri. Thus,
cutting into the narrow part of the ascending parietal gyrus on
the right side, there is a small sulcus which narrows the gyrus,
but at the same time produces a bend in it which increases its
extent.

In order to determine if any appreciable difference in the
transverse width of the 'motor' convolutions existed in normal
brains, measurements of four other brains were taken, and it
was found that though there was no constant difference, yet
considerable variation existed, and that the differences observed
in the ascending frontal convolutions on the two sides of the
brain taken from the person who had congenital absence of the
arm were not at all above the average. The differences in the
ascending parietal convolutions in this brain were, however,
slightly greater than those ascertained to exist in the other four
brains, and were more strictly localised.

From my observations I therefore imagine that no naked-eye
atrophy of the arm-centre of Sherrington and Grünbaum exists
in the brain I have described, and that it demonstrates the
fact that congenital deficiency of a limb may exist without the
co-existence of atrophy of that portion of the cerebral cortex
which presides over its movements. The two brains described
in the papers already referred to also support this statement,
and indeed it is reasonable to expect that absence of a limb
should not affect more than the lower neurone territory. Unfor-
tunately the spinal cord in this case could not be obtained for
examination.

The diminution in size of the ascending parietal gyrus opposite
the arm-centre of the frontal gyrus, which was present to some
extent in the two previously reported cases, and also in the

[PLATE III.

FIG. 1.

FIG. 2.

MR T. G. MOORHEAD.

present instance, is a fact of extreme interest, more especially since it has been shown that this area does not possess motor functions. I have had the advantage of seeing Professor Cunningham's collection of fœtal brains, in which it is seen that from the sixth month onwards the arm-centre of the frontal gyrus, and that portion of the parietal gyrus which lies immediately opposite to it, behind the fissure of Rolando, develop together, and form a marked elevation on the surface of the brain on either side of the shallow part of the fissure of Rolando. From the way in which they develop together it certainly suggests the conclusion that these two parts are functionally co-related; and though we have as yet no definite information regarding the function of the parietal part, I believe that Professor Cunningham inclines to the opinion that it acts as the receiving area for sensory impressions conveyed from the upper limb. If this be the case, it is possible to understand how such an area would be diminished in size in cases in which the upper limb was deficient.

Owing to the manner in which the specimen was preserved no microscopical examination of the cortex could be made, but in Gowers' case, and in that of Bastian and Horsley, no microscopical change could be detected. Whether improved methods of preparation and staining will show a distinction on the two sides in such cases remains a question for the future.

REFERENCES.

(1) "The Brain in Congenital Absence of One Hand," by W. R. Gowers, M.D., *Brain,* 1878.

(2) "Arrest of Development in the Left Upper Limb, in Association with an extremely small Right Ascending Parietal Convolution," by H. Charlton Bastian, M.D., F.R.S., and Victor Horsley, *Brain,* vol. iii.,1880–1881.

(3) Abstract from experimental work on the motor regions of the cerebral cortex, by Professors Sherrington and Grünbaum, *Lancet,* Nov. 21, 1901.

EXPLANATION OF PLATE III.

Fig. 1. Photograph of a cast of the arm of the individual referred to in the text.

Fig. 2. The two cerebral hemispheres of the same individual.

THE FORM OF THE HUMAN SPLEEN.

By R. K. Shepherd, B.Sc.

(From the Anatomical Department of the University College, Cardiff.) [1]

In ascertaining the exact shape which a soft pliable organ like the spleen possesses in the living body, one meets with very serious difficulties, as when the abdominal cavity is opened after death such structures lose their true shape, and one may get an altogether false idea of their outline when examining them in this manner. To surmount these difficulties, it has been customary within the last twenty or thirty years to harden these soft organs before examining them, and even before opening the cavity in which they are placed. This hardening has been done mainly by the injection of special hardening fluids, such as bichromate of potash,—this is nearly always used in combination with alcohol,—chloride of zinc, and within recent years, formalin.

Attention was first drawn to the enormous advantage to be obtained by hardening organs *in situ* by Professor His, and the models of the various viscera which he prepared were for many years the only ones well known. The method he used in the preparation of these was, the injection of from five to ten litres of a 5 per cent. to a 1 per cent. solution of chromic acid, under pressure.[2] The organs thus hardened were isolated, and models of them were prepared in plaster of Paris. Since 1878, when His made his first models, other hardening fluids have been tried; the one that has proved most successful, and is now generally advocated by all anatomists, including Professor His,[3] is a solution of formalin and alcohol. The viscera are hardened much more rapidly when it is employed; and further, they are not so œdematous as they are liable to be when other fluids are

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used. Professor Cunningham [1] in 1895 prepared models of the spleen and other abdominal viscera by means of the reconstruction method. In this method the body is frozen and cut in sections. The blocks or sections into which the body is cut are hardened by immersion in spirit, or spirit and formalin, and the separate pieces of any organ are removed, cast in plaster of Paris, or modelled in soft wood. The separate parts when joined together give a faithful representation of the organ. Cunningham's model of the spleen as prepared in this way differs in some important respects from His's.

The specimens from which the conclusions given in this paper have been drawn were hardened *in situ* before the abdominal cavity was opened. The bodies were hardened by intravascular injection of formalin, but in one case potassium bichromate was used instead.

General Form of the Spleen.

I have had an opportunity of examining about a dozen such spleens, and although such a number is too few for one to be able to dogmatise on any particular point, a good idea as to the more general features which the spleen presents can be easily obtained. When these spleens are placed side by side they are seen to show enormous variations in size and shape. Nevertheless in every case they are alike in possessing one, and only one, convex surface, which, when the spleen is in its place in the abdomen, rests against the diaphragm. This surface is relatively very large, and its convexity is most marked at the junction of its upper and middle thirds, for the upper part of this surface looks for the most part upwards, while the lower two-thirds looks backwards and outwards, and so at the junction of the two there is a marked convexity. As it is directed against the abdominal wall here formed by the diaphragm, this surface might well be called the *parietal surface* of the spleen. The rest of the surface of the spleen looks into the abdominal cavity and rests against other abdominal viscera; in contradistinction to the parietal surface, it may be termed the *visceral*

[1] "Form of the Spleen and Kidneys," *Jour. of Anat. and Phys.*, July 1895, p. 501.

surface. Unlike the parietal surface, the visceral surface is by no means even approximately uniformly curved, but it presents a number of areas or districts, which vary in the manner and amount of the curvature of their surfaces. These areas are usually three in number, and correspond to the so-called 'renal,' 'gastric' and 'basal' surfaces of Cunningham.[1] In every case one of these areas—the *gastric*—which is applied against the fundus of the stomach, can always be easily recognised, as it, and it alone, is always distinctly concave. In connection with the constant concavity shown by this surface it is interesting to note that Birmingham,[2] in his paper on the shape of the stomach, states that however empty the stomach may be, the fundus of the stomach does not collapse, but always retains a considerable amount of rotundity, its cavity being occupied by prominent folds of the thick mucous membrane. The presence of the hilus upon this surface assists in its identification. Another point which helps in the identification of this area is, that the border separating it from the parietal surface is sharp, and frequently crenated or notched.

The *renal area* is in nearly every case flat, or more rarely slightly concave from side to side. It is separated from the parietal surface and from the gastric area by thick rounded borders. The last of the three areas which compose the visceral surface of the spleen, the so-called 'colic' or 'basal' surface of Cunningham, is the most variable. The other areas vary but slightly in extent and in the amount of concavity or convexity which they present; this area, on the other hand, presents marked differences in different specimens. When it is well marked the area in question is usually in relation to the splenic flexure of the colon, and hence the term 'colic area' is applicable to it. In some cases this area is a relatively large triangular district occupying the lower end of the visceral aspect of the spleen, and having its apex directed upwards between the renal and gastric areas. Its extent may approach that of the renal area. In other cases the area in question becomes very narrow, or is so reduced that the gastric and renal areas are practically

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[1] *Loc. cit.*, pp. 505–506.

[2] "Points in the Anatomy of the Digestive System," *Jour. of Anat. and Phys.*, October 1900.

in contact from one end of the spleen to the other; in these cases the colic area is absent or reduced to a mere line or border, separating the gastric and renal areas in the lower part of their extent. (See fig. 1.)

A glance at the specimens, or at the outlines, which illustrate this paper will make it understood that upon the size and shape of this colic area will depend to a very large extent the shape which a spleen will present. If this area is large and well marked as it is in Cunningham's model, then the shape of
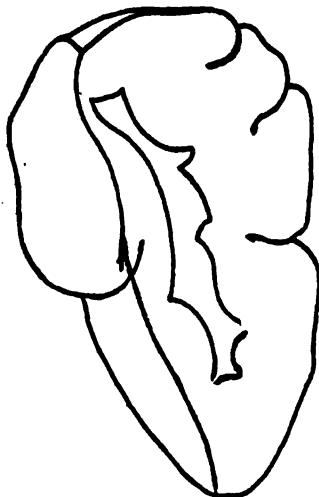
FIG. 1.—Fœtal spleen, showing well marked tubercle bounded below by a fissure.

This specimen shows the visceral surface divided into only two areas, viz., gastric and renal. These two areas are separated by the intermediate border, which is well defined above, but becomes flattened out as traced downwards below the tubercle.

The anterior border is well marked and has three notches in it; the posterior border has one notch only.

The hilus on the gastric area extends downwards below the level of the tubercle; the renal surface is flat. The lower end of ·the organ is smaller than the upper end, and is distinctly pointed.

the spleen is, as described by him, an irregular tetrahedron. In such cases the shape of the spleen might well be compared to that of a spore from a spherical capsule with a large convex surface looking outwards, and three triangular areas directed inwards towards the central part of the capsule. In the case of

such a spore these triangular areas would be in contact with the
corresponding areas of other spores. These three areas would
represent the gastric, renal and colic areas of the spleen, while
the large external convex area would correspond to the parietal
surface of the spleen. It must here be noted that Cunningham
applies the term 'base' or 'basal' surface to the colic area, and
'apex' to the upper angle of the spleen. The apex of the
tetrahedron as here described will correspond to Cunningham's
'internal basal angle,' and is the point where the three visceral
areas meet, while the base is the parietal surface. Now, turning
to the other form which the spleen sometimes exhibits, we note
that as the colic area becomes reduced, the spleen assumes the
outline of a three-sided figure, which might well be compared to
a segment, or fig, of an orange. Its surfaces, now three in
number, are—the parietal surface, and the gastric and renal
areas. The flat surfaces of the orange segment are represented
by the renal and gastric areas, while the outer convex surface of
the segment corresponds to the parietal surface in the case of
the spleen. As the upper end of the spleen in these cases is
found to be more massive than the lower end, the outline of the
organ resembles a segment of a somewhat pear-shaped body,
rather than a segment of a spherical body like an orange. It
will readily be understood that in this latter type of spleen the
parietal surface is somewhat oval, and each of the visceral areas
somewhat crescentic in outline; while in the tetrahedral form,
each of these areas is triangular in outline. When the outlines
of a number of spleens are examined it will be found that they
show nearly every stage in the transformation of the irregular
tetrahedron into a figure resembling a segment of an orange.
Of course, with a larger number of spleens, the series could
probably be made more complete, but as it stands it clearly
brings out the fact that what might be called the 'tetrahedral
type' of spleen becomes transformed into the 'segment type'
by the gradual decrease in size of the colic area, accompanied by
a simultaneous decrease in size of the lower end of the organ.
(See figs. 1, 2 and 3.)

These differences in form presented by the spleen appear to
depend to a very large extent upon the condition of distension
or contraction of the neighbouring structures. It is only to be

expected that the amount of surface in relation to the stomach
or the colon should depend largely on the relative sizes or
amount of distension of these parts of the alimentary canal. It
is to be regretted that the condition of the stomach and colon,
before removal of the spleen, was not noted in many cases; not-
withstanding this, however, it is practically certain that the
variations in the shape of the spleen were intimately associated
in some of the cases, at all events, with definite conditions of
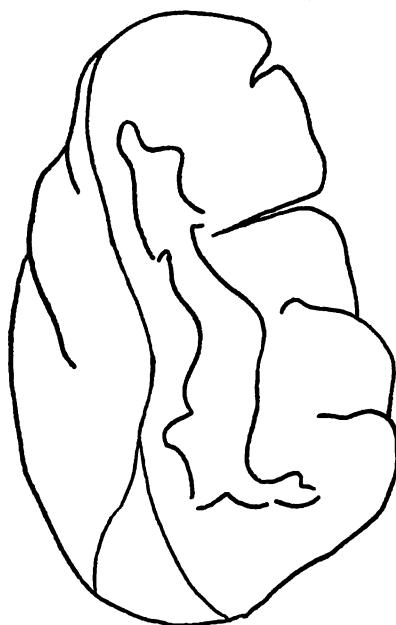
FIG. 2.—An adult spleen, showing renal and gastric areas, and a small colic area ;
this spleen is well notched, and the notches are in every case save one con-
tinued into fissures in the parietal, renal and gastric surfaces. The anterior
angle is not prominent, the most anterior point being situated higher up on
the anterior border.

the neighbouring viscera. It would now appear to be a well
established fact that when the stomach is empty the colon rises
up to take its place and fill the gastro-colic chamber; as the
colon rises up to occupy a position formerly filled by the stomach,
it necessarily comes more fully into relation with the spleen.
The gastric area is therefore reduced to the advantage of the

growing colic area. On the other hand, as the stomach becomes distended the reverse occurs, the colon sinks, and the colic area of contact becomes reduced, so that finally merely the lower part of the border separating the gastric and renal areas is in relation to the colon. The increase in width and thickness of the lower end of the spleen, which is especially seen in spleens where the colic area is large, is also to be associated with the upward thrust of the colon, in conjunction with an empty or almost empty stomach. It is worth while noting that the models prepared by His and Cunningham fully support this view. In His's model the stomach is distended and the colon not much so; here we find a very minute colic area, and the spleen is of the orange-segment type. In Cunningham's model, on the other hand, the stomach is empty and the colon very greatly distended, and associated with these conditions there is a large colic area and a tetrahedral type of spleen.

One would perhaps expect the extent, or the presence even, of the colic area to depend to some degree upon the form and size of the spleen itself, e.g., a short, small spleen might be less likely to have a colic area than a long, big one; nevertheless, among the specimens examined, there have been small spleens showing well marked colic areas, and large ones showing no such area at all. It will thus be seen that the differences to be observed in His's and Cunningham's models do not indicate that in either case an abnormal or atypical spleen has been present, but rather that each observer has modelled a form of spleen which normally occurs in man. Between the forms represented by the two models every possible intermediate stage may be found, and the marked differences appear to be due to the fact that the condition of the neighbouring viscera—stomach and colon—was exactly opposite in the two cases. One important distinction does exist, and has been duly noted by Cunningham; it has to do with the relation of the renal surface to the kidney,[1] and will be dealt with later on.

As the difference between the two forms of spleens is due to a difference in the amount of distension of the stomach and colon, intermediate stages are easily obtained in which variations in the amount of colic area are seen, due to the variations in the disten-

sion of the stomach and colon. From an examination of these intermediate forms of spleens the following changes may be said to occur in the transformation of a three-sided orange-segment type of spleen into the tetrahedral type of spleen :—First, the lower portion of the border separating the gastric and renal areas is blotted out—obliterated by the upward pressure of the colon ; and at the same time the lower end of the spleen is pushed upwards against the portion above by the distending colon, thus widening and thickening the lower end of the organ. As the colon becomes more distended the lower end of the spleen becomes pushed outwards and upwards, so that the visceral surface of the lower end comes to look downwards as well as inwards, and thus becomes separated off from the rest of the visceral surface by definite borders. When the colon becomes very distended this surface comes to look directly downwards, and the lower end of the spleen is greatly thickened. This must only be considered to be a general account of the changes that occur : a far larger number of bodies would have to be examined before a really accurate account of the changes could be given. The fact that it is the hollow organs which indent or groove the solid ones appears to have been recognised first by His when conducting his early experiments upon hardening viscera *in situ*. This observation has been abundantly confirmed by other workers.

Borders of the Spleen.

Every spleen, whichever type it belongs to, presents three borders separating the three constant surfaces or areas, viz., the parietal, the gastric, and the renal. These three borders are called anterior, posterior and intermediate, and correspond to Luschka's ' margo crenatus,' ' margo obtusus,' and ' margo intermedius.' They separate the parietal surface from the gastric and renal areas, and the gastric and renal areas from one another. (See fig. 1.)

The *intermediate border* runs from the upper end of the spleen downwards, separating the renal and gastric areas. The border ends either at the lower end of the spleen when there is no colic area, or when this area is distinct.

the border in question ends at Cunningham's 'internal basal angle,'[1] where it bifurcates into the two borders which separate the colic area from the renal and gastric areas respectively. The border is rounded especially in its lower portion; its upper part, much more acute and distinct generally, overhangs to a slight extent the upper part of the gastric area. The intermediate border is not straight, but is usually slightly curved, having the convexity of the curve looking backwards and inwards; this being so, the border is gently continued at the upper end of the spleen, or superior angle — Cunningham's ' apex '—into the anterior border of the spleen. (See fig. 3.)

At some distance from its upper end the intermediate border often presents a tubercle of varying size; this tubercle is present in a large proportion of spleens, whatever their shape, and varies from a slight, hardly noticeable elevation, to a prominent tubercle, standing well out from the rest of the organ. When well marked the tubercle is sharply defined below, while superiorly it is continued into the prominent upper part of the intermediate border. In some of these cases the intermediate border might almost be said to end in this border, as below it the border is so flattened that it cannot be satisfactorily traced. On the other hand, in those specimens which show no tubercle, the intermediate border is not flattened out inferiorly, but can be easily traced to the apex of the colic area. In connection with this tubercle, it should be noted that there is generally to be seen a fissure, either extending from the posterior border, from a point usually situated in its upper half, towards the tubercle, or encircling it below. (See fig. 1.)

Whether the tubercle has any developmental or embryological significance, it is not possible to say at present; it is certainly very well marked in many foetal spleens. My observations seem to show that this tubercle fits in above the tail of the pancreas, which rests against the flattened area below. When the tubercle is absent, the intermediate border is not flattened inferiorly, and so I am inclined to believe that the presence of the tubercle is to be associated with a close relationship of the tail of the pancreas to the spleen. If this is correct, one would expect the tubercle to be absent in cases in which

[1] *Loc. cit.*, p. 505.

the tail of the pancreas did not reach the spleen, or in which this part of the gland was feebly developed, I have found the tubercle to be crossed either by the splenic artery itself, or by one of its branches going to the upper end of the hilus. A groove for the vessel may sometimes be seen upon the tubercle in hardened specimens.

The *anterior*, or *crenated border*, runs from the upper end of the spleen downwards and forwards, separating the gastric area from the parietal surface. This border ends below, either at the lower end of the spleen by joining the posterior and intermediate borders when there is no colic area, or at the anterior angle of the spleen when the area in question is present. This border is the most acute of the three primary borders, and is continuous with the intermediate and posterior borders at the upper end of the spleen. Its upper third is directed more or less outwards, its lower two-thirds downwards and forwards; as a consequence of this, the most anterior point of this border is generally somewhere about its lower end; this point is Cunningham's 'anterior basal angle,' and is usually very prominent in a tetrahedral type of spleen, though this is not always the case.

A very characteristic point with regard to the anterior border is the notching it often shows all along its course; this appearance gave rise to Luschka's name for it—' margo crenatus.' The notching is seen in nearly every spleen, the actual number of notches being extremely variable; in some cases five, or even more, have been found, but on the whole, the average number of notches is about two. The notches, which vary in depth from a quarter of an inch to an inch, or even more, may or may not be continued into fissures on the parietal surface; about half of them are usually so continued. The fissures usually run downwards, backwards and inwards, and in some cases they stretch right across the parietal surface so as to cut into and notch the posterior border of the spleen.

The *posterior border* is placed between the renal area and the parietal surface. It runs from the upper extremity of the organ, first of all outwards and backwards, and then downwards, either to the lower extremity in the orange-segment type of spleen, or to the posterior angle in the tetrahedral type of

spleen. At this angle the posterior border meets the border separating the colic and renal areas; Cunningham calls this point the 'posterior basal angle.' The posterior border is thick in the whole of its extent; in its upper part, this border seems to fade away so that there is no definite line of separation between the renal area and parietal surface. The border is sometimes notched like the anterior one, only not to such a great extent; in nearly all cases, however, the notches, when
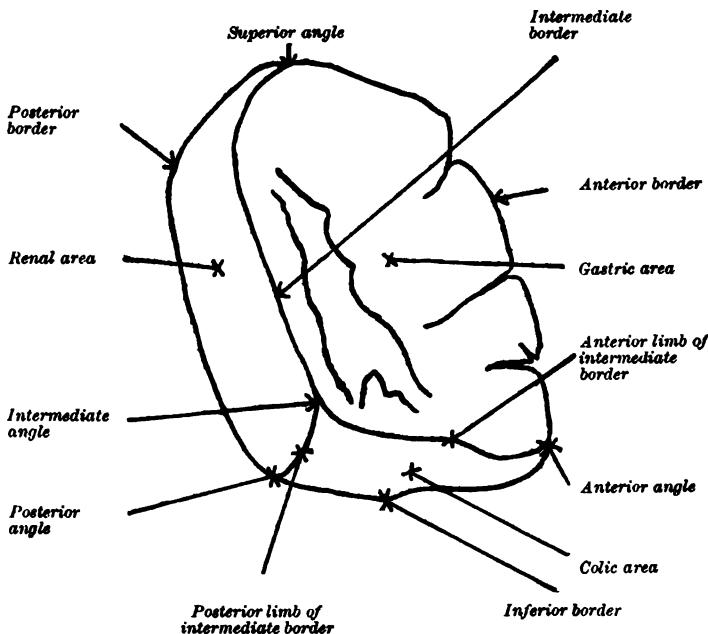
FIG. 3.—A child's spleen. This is a fairly typical tetrahedral spleen; it has no tubercle, and only shows notching on the anterior border. The anterior angle is prominent.

present, are continued into fissures on the parietal surface, as Parsons[1] has recently pointed out, and in some they are also continued into fissures on the renal area, such fissures being directed towards the tubercle on the intermediate border. The fissures on the parietal surface are directed upwards, forwards and slightly outwards. As a rule, not more than one fissure

[1] "Notches and Fissures of the Spleen," *Jour. of Anat. and Phys.*, vol. xxxv. p. 422.

is to be seen on the parietal surface, but two are by no means infrequent.

These three—the anterior, posterior and intermediate—may be called the three *primary borders*, since they are always present; there are, however, three *secondary borders* which are to be seen in spleens of the tetrahedral type, or those showing a colic area. These latter borders serve to delimit the colic area, and separate it from the renal and gastric areas and from the parietal surface. (See fig. 3.)

The *inferior border* is the best marked of these secondary borders; it stretches from the anterior angle of the spleen to the posterior angle, and is placed between the colic area and the parietal surface. This border may be notched like the anterior and posterior borders, but the notching, which is insignificant, is of very rare occurrence. The other two borders are by no means distinct save in specimens showing a well marked colic area, and in these the border separating the colic and gastric areas is the better marked of the two. These two borders and the intermediate border meet internally at a point —the *intermediate angle*—Cunningham's 'internal basal angle' —which is usually very indistinct except in typically tetrahedral spleens. This angle forms the apex of the flattened tetrahedron, whose base is the parietal surface. It has already been mentioned that the points where the two borders separating the colic from the renal and gastric areas meet the posterior and anterior borders respectively are called the *posterior* and *anterior angles* of the spleen. It should be noted here that the anterior angle is not always the most anterior point of the spleen; in some cases the most anterior point is situated higher up on the anterior border, and in these cases the anterior angle is by no means distinct.

The spleen has two extremities — an upper and a lower; the upper end or *superior angle* of the spleen is posterior and internal to the lower, as well as being superior to it. The upper end of the spleen is rounded, the superior angle being incurved.

The lower end varies from being sharp and pointed in a 'segment type' of spleen to wide and thick; in fact, it becomes a whole surface when the spleen is tetrahedral in outline. The notching of the spleen has attracted some attention recently.

In England, Parsons[1] has recorded a number of observations, made chiefly in the post-mortem room, on normal spleens. The statements made in this paper are, as far as they go, in agreement with his results, but he has also noted cases in which fissures were present on the parietal surface only, not extending to the borders bounding the surface. He concludes that the notching is, in a general way, dependent on the arrangement of the large blood-vessels. He finds that in some animals, such as the seal, the notches seem to correspond to the blood-vessels entering the hilus; but Parsons admits that in man, at all events, the notches do not show a dependence upon the distribution of the vessels in all cases. Another theory regards the notches as having developmental significance, but unfortunately there is no trace of a primitive lobulation in the human fœtal spleen, unless except possibly the tubercle of the intermediate border is to be looked upon as an indication of primitive lobulation. Further, Parsons states that the notches are relatively less marked in the fœtus than in the adult, and also the number of the fissures seems to increase as adult life is approached. Lobulation, too, is not seen in lower vertebrates till we get back to the elasmobranchs, and even then it is not found in every species; so at present, at all events, this theory must be discarded.[2]

It has been further suggested that the notches are due to processes of peritoneum passing to the notches from the peritoneal ligaments, and thus acting as a check on growth at such points. Such peritoneal processes are occasionally met with in man, but are comparatively rare, and so could not by any means account for the large number of notches that are frequently met with. Up to the present, therefore, no satisfactory theory as to the origin of the notches has been propounded, none of those mentioned above being satisfactory.

Surfaces of the Spleen.

A general description of the surfaces of the spleen has already been given; a few minor points of detail have yet to be mentioned.

[1] *Loc. cit.*, p. 416.   [2] *Loc. cit.*, p. 426.

The *parietal surface* is in relation to the diaphragm, being separated by the diaphragm and the thin basal margin of the left lung from the ninth, tenth, and eleventh ribs; the longest diameter of the spleen corresponds with the axis of the tenth rib; it may have a vertical fissure in the middle of the surface, as already mentioned; such fissures are, however, of rare occurrence.

The *gastric area* is in relation to the fundus of the stomach; it is not uniformly concave, the concavity increasing as we pass towards the upper end of the spleen; the concavity is greatest immediately to the outer side of the tubercle of the intermediate border. In this area is placed the hilus of the spleen. This lies about half an inch to the outer side of the intermediate border, and extends from the level of the tubercle right down to the lower end of the border. The hilus may be broken up into three or four separate portions, or it may be one continuous cleft-like depression. The splenic branches of the splenic artery enter the spleen in three or four main groups; the highest-up group enters in the deep concavity to the outer side of the tubercle. A secondary hilus is sometimes seen at the upper end of the spleen; it extends from the superior extremity of the spleen to the level of the tubercle along the line of attachment of the lieno-phrenic ligament, and lies above and behind the primary hilus of the spleen; the arteries that enter the spleen in this part are derived either from the splenic artery or from the left inferior phrenic artery; the surface of the organ is not depressed to form a cleft or fissure where they enter.

The *renal area* is in relation to the left kidney. His made this surface deeply concave both in its long diameter and from side to side, and his models show this surface applied against the outer border of the kidney. Cunningham, on the other hand, makes his renal surface flat and even, and shows it to be applied against the anterior surface of the kidney. In all the spleens examined in connection with this paper the renal area has been found flat, or a trifle concave in one or two instances. In all the cases it was in relation to the upper part of the anterior surface of the left kidney in its outer part; in one or two cases it was also related to the left suprarenal capsule.

In the fœtal abdomen this surface is related to the left supra-renal capsule rather than to the kidney.

The *colic area* is in relation to the summit of the splenic flexure of the colon ; when present it is triangular in outline, and is usually flattened ; in one or two cases where the spleen is markedly tetrahedral, this area is slightly concave; except in such cases the colic area is not well marked off from the gastric and renal areas, the lines of demarcation being indefinite. As might be expected from the fact that the colic area of tetrahedral spleens is simply a cut-off part of the gastric area of the segment type of spleens, one or two branches of the splenic artery are occasionally found to enter the spleen in this area. In some of the cases examined the spleen has not been in direct contact with the other viscera, but was separated from them by a mass of fat. This is well seen in a frozen section in the collection at Cardiff. It is important to note that even in these cases the impressions were always well marked.

Attachment of Peritoneum to the Spleen.

Peritoneal ligaments, or omenta, pass to the spleen from three other structures in the abdomen. First, there is the *gastro-splenic omentum* passing from the fundus of the stomach to the hilus of the spleen ; processes of peritoneum pass from this omentum in rare cases to the anterior notches. In all cases where the anterior angle is well developed a process of peritoneum passes to the angle, and in some cases the angle is curved in-wards. Whether this is due to the pull on the angle by the omentum or not is doubtful. Second, there is the *lieno-renal ligament* passing from the anterior surface of the kidney to the hilus of the spleen. Third, there is the *lieno-phrenic ligament* passing from the under surface of the diaphragm to the upper end of the spleen, being attached along the upper portion of the intermediate border, behind and above the gastro-splenic omentum, with which it is continuous, and also with the gastro-phrenic ligament. This ligament is not always present.

The following averages were obtained from an examination of eight adult spleens, the measurements are in inches. The spleens were weighed after hardening.

Average length of spleen,	.	.	.	$4\frac{5}{8}''$
Greatest length,	.	.	.	$5\frac{7}{8}''$
Least length, .	.	.	.	$4''$
Average breadth of spleen,	.	.	.	$3''$
Greatest breadth,	.	.	.	$3\frac{3}{4}''$
Least breadth,	.	.	.	$2\frac{1}{2}''$
Average thickness of spleen, .	.	.		$1\frac{7}{8}''$
Greatest thickness, .	.	.	.	$2\frac{1}{2}''$
Least thickness,	.	.	.	$1\frac{1}{4}''$
Average weight of spleen,		.	.	6 oz.
Greatest weight,	.	.	.	$9\frac{1}{4}$ oz.
Least weight, .	.	.	.	4 oz.

The three outlines accompanying this paper are selected from a series which have been drawn from the spleens after removal from the body, by a camera lucida. The table gives the chief particulars of all the cases. In each case the weight and extreme length is given. Fœtal spleens are marked with a star.

Since the above paper was written I have had the opportunity of observing seven models prepared by Steger at Leipzig, under the direction of Professor His, illustrating the anatomy of some of the abdominal viscera.

    I. *16 jähr Mädchen. Schnürmagen.* Stomach is distended, spleen is of the orange-segment type.

   II. *16 jähr Mann. Kellner.* Stomach is distended, spleen is of the orange-segment type.

 III. *40 jähr Frau im 5 Monat schwanger.* Stomach is moderately distended, the colic surface is seen.

 IV. *40 jähr Frau. Schnürmagen.* Stomach is moderately distended, colic surface seen ; markings of ribs seen on parietal surface,

  V. *20 jähr Mann. Normal.* Stomach is contracted, only in contact with a very limited area on the spleen ; there is a large colic area not sharply delimited.

 VI. *56 jähr Mann. Trinker.* A tetrahedral spleen ; the gastric area is only slightly in contact with the stomach, the rest being related to the large or small intestine.

VII. *25 jähr Frau im 2 Monat schwanger.* Stomach is moderately distended ; there is a small colic area.

All these bear out the statements in this paper except No. VI., which is abnormal.

[TABLE.

TABLE *showing Measurements and Observations on Thirteen Spleens.*

Number.	Notches: Anterior Border.	Notches: Posterior Border.	Notches: Inferior Border.	Fissures: Anterior.	Fissures: Posterior.	Measurements: Extreme Length.	Measurements: Weight	Tubercle on Intermediate Border.	Process of Peritoneum to Anterior Angle.	Renal Surfaces.	Secondary Hilus present.
1*	(fig. 1) 3	1	0	2	2	2"	2 oz.	yes	...	flat	yes
2	2	1	0	0	1	4¾"	4¼ oz.	yes (very small)	...	flat	no
3	0	1	0	0	1	4¾"	7½ oz.	yes	no	concave	yes
4	(fig. 2) 4	2	0	5	1	4½"	5¼ oz	yes	yes	concave	no
5	2	0	0	0	0	4½"	9¼ oz.	yes	yes	slightly concave	yes
6	2	2	0	1	1	5⅜"	6½ oz.	yes	yes	flat	no
7	1	1	1	3	0	4¼"	4 oz.	yes	no	slightly concave	yes
8*	3	0	1	1	0	2⅞"	¾ oz.	no	yes	slightly concave	no
9	(fig. 3) 3	0	0	4	0	3¼"	2¼ oz.	no	no	flat	no
10*	2	0	1	0	0	1⅞"	½ oz.	yes	no	slightly concave	no
11*	3	0	0	0	0	1⅛"	¼ oz.	no	no	flat	no
12	1	1	0	0	1	4⅞"	7½ oz.	no	no·	flat	no
13	4	1	0	2	1	4"	4 oz.	yes	yes	flat	no

Summary.

As a result of the observations recorded, the following con-clusions seem justified :—

(1) The normal spleen may be said to exhibit two chief surfaces—Parietal and Visceral—the latter being divided into two or three areas.

There are two chief types of spleen form to be met with in hardened subjects. In the one type the spleen is shaped like the segment of a pear, and possesses a *parietal surface*—the convex outer surface of the segment and *two visceral areas*—the two flat surfaces of the segment. The inner of these areas is in contact with the kidney and the outer with the stomach; they are called the *renal* and *gastric areas*. His's model represents this type of spleen, if one or two minor points of detail are overlooked. In the other type, the spleen is shaped like an irregular tetrahedron and has a *parietal surface*—the base of the tetrahedon; and *three visceral areas* which meet internally at a point—the *intermediate angle*—the apex of the tetrahedron. These areas are the *renal, gastric* and *colic areas*, the last named being in contact with the splenic flexure of the colon.

(2) The gastric and renal areas are separated by a border which is always well marked—the *intermediate border*. The gastric area is marked off from the parietal surface by the *anterior border*, also well marked, while the renal area is separated from the parietal surface by a border which is well marked, especially in its lower portion—the *posterior border*. These three borders are alone to be met with in the 'segment' type of spleen; in the tetrahedral type there are three second-ary borders as well as the three just mentioned. The inter-mediate border ends below by bifurcating, so as to enclose the colic surface; these two limbs into which it divides are not at all well marked except in typical tetrahedral spleens. In these the colic area is separated from the parietal surface by a secondary border, which is fairly well marked—the *inferior border*.

(3) The lower end of the spleen varies a good deal in shape,

being pointed in the 'segment' type, and wide and thick in the tetrahedral type; in fact, in this type it becomes a whole surface—the colic surface.

(4) The two types of spleen appear to be due to differences in the state of distension of the surrounding organs, chiefly the stomach and colon. When the stomach is distended and the colon is empty, the spleen is shaped like the segment of an orange. When the conditions are reversed, the colon being distended and the stomach empty, the spleen is tetrahedral in shape.

(5) A spleen belonging to one of these types becomes transformed into the other type simply by a change in the condition of the colon and stomach, and this transformation probably takes place periodically in the living body.

(6) The renal area on the spleen is flat, and is applied against the upper part of the anterior surface of the left kidney in its outer part, as described by Cunningham; in some cases it is also related to the left suprarenal capsule. In the foetal abdomen this area is rather in relation to the left suprarenal capsule than to the kidney.

(7) A tubercle is often found on the intermediate border; when present the portion of the border below it is usually very much flattened, and is in relation to the tail of the pancreas. When the tubercle is absent there is no flattening; the presence of a marked tubercle appears to be associated with a close relationship of the tail of the pancreas to the spleen.

(8) Notching of the borders and fissures of the surfaces were noted; in nearly every case the anterior border was notched in two or three places; the posterior border was also notched, but not nearly so frequently as in the case of the anterior border. In nearly every one of the specimens examined which showed posterior notches, the notches were continued into fissures on the parietal surface. The inferior border was found notched in two instances only. No connection was noticed between the arrangement of the notches and the mode of distribution of the blood-vessels. The notches and fissures do not repeat any early lobulation of the organ.

(9) In nearly every case where the spleen is of the tetrahedral type, a process of peritoneum is seen passing to the anterior

angle of the spleen; in these cases the angle is generally incurved. What this is due to is doubtful.

(10) In some spleens a peritoneal ligament is seen passing from the upper end of the spleen to the under surface of the diaphragm. It is called the *lieno-phrenic* ligament. One or two arteries enter the spleen along the line of attachment of this ligament.

PRELIMINARY NOTE ON THE POSITION OF THE GALL-BLADDER IN THE HUMAN SUBJECT.

By E. SCOTT CARMICHAEL, M.B., F.R.C.S.E., *Senior Demonstrator of Anatomy, New School, School of Medicine of the Royal Colleges, Edinburgh.*

THE ever increasing frequency with which abdominal viscera are being subjected to surgical treatment renders a more exact knowledge of their topographical anatomy of great practical importance.

The difficulties of anatomists in definitely localising viscera which are constantly varying in their shape, and, to a certain extent, in their position within the abdominal cavity, are great; but much can yet be done by observing the more common variations to ascertain their anatomical position more approximately.

During the last year I have had the opportunity of making observations on a considerable number of abdomens in the dissecting-rooms. These are, as a routine practice, hardened by the injection of formalin into the stomach, bladder and rectum, a method carried out by Dr R. J. A. Berry on all subjects for dissection.

These observations have been largely directed towards ascertaining the position of the gall-bladder, chiefly on account of some pathological work which is at present being carried out on that viscus.

The position of the gall-bladder in the abdomen is stated in standard anatomical text-books to be situated opposite the ninth right costal cartilage.

From a few observations on these formalin-hardened bodies, one is struck with, firstly, the irregularity in length and position of the 9th costal cartilage, making it not in any sense a reliable fixed point; and secondly, the frequency with which the gall-bladder has no close relationship to the cartilage.

To the surgeon particularly it is extremely difficult to define

the limits of the 9th costal cartilage, more especially as regards its tip or termination.

In ten cases examined, the length of the cartilage varied from 5 to 12 cm., the average being 7·5 cm. or 3 inches—a considerable distance in which to localise the gall-bladder in a horizontal direction.

The tip of the cartilage is found to vary very considerably in the height to which it extends on the costal margin.

In taking the tip of the cartilage as a definite point, I found that in only one out of the ten cases did the gall-bladder lie behind it, while in four it lay from 2 to 4 cm. above it under the costal margin, and the remaining five 2·5 to 8 cm. below it, showing in these ten subjects a difference of nearly 5 inches (12 cm.) in its position in a vertical direction.

Its variations in a horizontal plane, as measured by taking the right lateral line of Addison as the fixed point, showed that in seven cases tested, the gall-bladder lay from 1 to 6 cm. external to that line, while in another case it lay as much as 9 cm. outside the right lateral line, and parallel to the 11th costal cartilage.

Of the seven cases referred to, the lateral position of the gall-bladder varied in five cases from 2 to 4 cm. outside Addison's right lateral line.

Observations on a larger number of bodies in the dissecting and post-mortem rooms, with or without formalin injection, will doubtless lead to a more definite localisation of this viscus, not to a fixed point, but to a fixed line, such as the right lateral line of Addison, whose method of abdominal localisation lends itself as a more reliable means of fixing the position of an abdominal viscus.

The variation in position of the gall-bladder is much greater in the vertical than in the horizontal direction, and would suggest some vertical line along which this variation extends as the better means of localising its position.

Addison's lateral line in all cases examined touches the clavicle considerably internal to its mid-point, and apparently at a fairly constant distance. This distance in five cases observed was from 3 to 4·5 cm.

The gall-bladder, lying as it does in about 90 per cent. of

cases external to Addison's right lateral line, corresponds very much in its position to that line to the mid-clavicular point.

The following table of five cases will illustrate my meaning:—

1. Gall-bladder lay 2·5 cm. outside Addison's Line.						Mid.-clav. point lay 4 cm. outside Addison's Line.				
2.	,,	,,	3·5 cm.	,,	,,	,,	,,	4·5 cm.	,,	,,
3.	,,	,,	3 cm.	,,	,,	,,	,,	3 cm.	.,	,,
4.	,,	,,	2 cm.	,,	,,	,,	,,	4·5 cm.	,,	,,
5.	,,	,,	2 cm.	,,	,,	,,	,,	3·5 cm.	.,	,,

The measurements were made from the lateral line to the nearest point on the fundus. The breadth of the fundus of the gall-bladder in these cases was from 2 to 3 cm., so that a vertical line dropped from the mid-clavicular point crossed in all these cases some part of the fundus of the gall-bladder.

It is my intention, by further observation, to investigate the relationship of the gall-bladder to the lateral line of Addison, or to the mid-clavicular line, both of which are more fixed and more easily obtainable to the practical surgeon than any point on, or even the whole of, the 9th costal cartilage.

My conclusions on these few observations are:—

Firstly. That the statements in text-books localising the gall-bladder as lying opposite the 9th costal cartilage are in upwards of 75 per cent. of cases erroneous.

Secondly. That the 9th costal cartilage itself is a very unreliable fixed point, on account of its variability in length and extent.

Thirdly. That any localisation of the gall-bladder must be rather by a vertical than a horizontal line.

Fourthly. That the gall-bladder lies in 90 per cent. of cases outside Addison's right lateral line.

Fifthly. That the gall-bladder is crossed at its fundus in most cases by a vertical line drawn from the mid-point of the clavicle.

THE DEVELOPMENT OF THE HEAD MUSCLES IN SCYLLIUM CANICULA. By F. H. Edgeworth, M.B., B.Sc., Assistant Physician to the Bristol Royal Infirmary. (Plates IV.—X.)

(From Prof. Fawcett's Laboratory, University College, Bristol.)

THE theories of Balfour and v. Wijhe on the morphological position of the muscles developed from the walls of the head-cavities lying between the gill-clefts in the Elasmobranch head are so divergent—the former holding that they are somatic, the latter that they are splanchnic structures—that the subject appeared worthy of reinvestigation, especially in view of the fact that what is true of the Elasmobranchs probably holds for Vertebrates in general.

The following is a summary of their statements. The head-cavity of Elasmobranchs was discovered by Balfour,[1] who describes it as a slit developed in the mesoblast sheet lying on either side of the forepart of the alimentary canal.

The successive formation of the gill-clefts, from before backwards, divides this head-cavity into portions lying in the respective gill-arches. The head-cavity lying in front of the hyomandibular cleft divides spontaneously into two parts, a posterior in the mandibular arch, and an anterior, or premandibular, situated close to the eye. The premandibular cavity is prolonged ventrally and meets its fellow below the brain. Balfour was of opinion that the eye-muscles would be found to be developed from the walls of this cavity. The mandibular cavity becomes spatulate in shape, forming a flattened cavity, dilated dorsally, and produced ventrally into a long thin process parallel to the hyomandibular gill-cleft. The upper dilated part atrophies, whilst the splanchnic wall of the lower part thickens. There is a similar section of the head-cavity in each of the remaining arches, though a dorsal dilated portion (which soon atrophies) is present in the hyoid section only. Whilst the cavities of the head-cavities in the gill-arches collapse, their walls thicken, and become converted into muscles—"their exact history I have not followed out, but they unquestionably become the m. constrictor superficialis and m. interbranchialis, and probably also the m. levator mandibulæ and other muscles of the front part of the head." The fact that the walls of the sections of the body-cavity in the head become converted into muscles "renders it almost certain that we must regard them as equivalent to the muscle-plates of the body which originally ·contain, equally with those of the head, sections of · the body-cavity."

[1] This Journal, vol. x., 1880.

Balfour also described, behind the auditory involution, a few longitudinal muscles, which he was inclined to think were a part of the trunk system of muscles overlapping the back part of the head.

A little later, Marshall[1] confirmed in part the suggestion of Balfour, by showing that the walls of the premandibular cavity develop into the rectus superior, internus and inferior, and probably the inferior oblique, eye-muscles. He also gave good reasons for thinking that the external rectus is developed from the dorsal dilated portion of the hyoid cavity. He did not trace the origin of the superior oblique.

In the following year v. Wijhe[2] published his important paper on the development of the muscles and nerves of the Elasmobranch head. The following is his tabular statement of the development of the muscles : —

Aus dem Myotome stammende Muskeln	Ventrale Nervenwurzel	Visceral- bogenhöhle	Dorsale Nervenwurzel
Segmente		Aus dem Pericardium und den Wänden der Visceralbogenhöhlen stammen¹e Muskeln.	
1 Rect. sup. int. inf. obliq. inf.	iii . .	? . .	oph. prof.
2 Obliq. sup.	iv . .		v. (Nach Abzug des oph. prof.)
3 Rect. ext.	vi . .		} Aucusticofacialis
4 0	0 . .	Kiemen und Kiefermuscu- latur mit Ausnahme des Sternohyoideus	
5 0	0 . .		glossopharyngeus
6 Sehr rudimentär .	nicht wahrgenommen		
7 ⎱ Von Schadel zum			⎱
8 ⎰ Schultergurtel			} vagus
9 ⎰ ziehende Muskeln nebst dem vor- dersten Theile der Sternohyoideus			⎰

The 4th and 5th myotomes altogether atrophy, whilst the 6th of the latest stage seen was very rudimentary, and so probably atrophies. The development of the ventral longitudinal muscles is as follows— "Das rudimentäre sechste" (*i.e.* myotome) "liegt noch stets an der Innenseite des R. branchialis I Vagi, aber die folgenden haben sich dorsalwärts verlängert, ebenso wie die Myotome des Rumpfes. Ausserdem kommt eine ventrale Verlängerung dem hintersten Kopf-

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[1] *Quart. Jour. Micr. Sci.*, vol. xxi., 1881.

[2] " Ueber die Mesodermsegmente und die Entwickelung der Nerven des Selachierkopfes," *Verhand. der K. Acad. der Wissen. zu Amsterdam*, 1882.

myotome zu, fehlt dem vordersten (dem 1sten bis 6ten) aber vollstän-
dig. (Note.—Ob das siebente und achte Myotom sich in späten Stadien
auch noch weit ventralwärts ausstrecken habe ich nicht ermittelt.)
Schon gegen das Ende des Stadium K. fängt die ventrale Verlänge-
rung, sowohl des hinstersten Kopfmyotome als die der vorderen
Rumpfmyotome sich nach vorn umzubiegen an. Im Stadium O
haben diese Verlängerungen, welche später selbstständig werden, schon
ziemlich weit nach vorn vorgegriffen. Aus ihnen entwickelt sich der
Musc. coraco-hyoideus, welche also genetisch von der ubrigen, aus den
Seitenplatten stammenden Kiemen- u. Kiefermusculatur, ganz
verschieden ist. Der Musc. coraco-branchialis + coraco-mandibularis
hat eine ganz andere Entstehungsweise als der coraco-hyoideus. Es
entwickelt sich nämlich aus der unpaaren vorderen Verlängerung des
Pericardiums, dessen Höhle, wie wir gesehen haben im Stadium J mit
den Höhlen der Visceralbogen communicirt. Nach dem Stadium K
fängt diese vordere Verlängerung zu obliteriren an; die Zellen ihrer
Wände werden Muskelfasern und im Anfang des O ist der ganze
Höhle geschwunden; ihre muskelösen Wände sind zusammengekom-
men, und bilden die Anlage des Musc. coraco-mandibularis + coraco-
branchialis. In später Stadien ist derselbe immer leicht von dem
Musc. coraco-hyoideus zu unterscheiden. Die Nebenzweige, welche
ersterer zu den Visceralbogen abgiebt, sind aus den Unterenden der
Wände der Visceralbogenhöhlen entstanden."

Balfour's view that the cavities in the gill-arches are homologous
with those of the somites of the trunk is untenable. "Es scheint mir
sicher das hauptsächlich die Verthältnisse im Stadium J beweisen dass
sie" (i.e. the cavities in the gill-arches) "dagegen mit einem
Abschnitt der bleibenden Leibeshöhle des Rumpfes zu homologisiren
sind; ich stelle die Gründe zusammen. In der ersten Hälfte des
Stadium J hat sich die primäre Leibeshöhle in die Höhlen der Myotome
und die secundäre Leibeshöhle differenzirt, durch die Trennung der
Somite (mit Ausnahme des 2ten) von die Seitenplatten; die Höhlen
in den Visceralbogen erstrecken sich nun nicht über die untere
Grenze der Somitenplatte (resp. Myotomenplatte) und sind von den
Höhlen der Somiten (mit Ausnahme derjenigen des zweiten) getrennt;
sie communiciren aber mit den Pericardiumraume. Ausserdem werden,
wie wir in Stadium I gesehen haben, die Kiementaschen unter der
Somitenplatte angelegt. Wären dagegen die Höhlen in den Visceral-
bogen mit denen der Somiten vergleichbar, so müssten sie alle
ursprunglich mit einer der letzteren (oder der Myotome) in Ver-
bindung stehen, und dies ist für diejenigen der hinteren Visceralbogen
nicht der Fall."

Before describing the results of my own observations, one or
two remarks may be made concerning these various statements.
The IXth nerve—that of the 1st branchial segment—is that
of v. Wijhe's 5th head segment. There are thus four segments
anterior to it; whilst according to Balfour there are only three

—the premandibular, mandibular and hyoid. Marshall showed that from the premandibular segment the superior, internal and inferior rectus, and the inferior oblique muscles develop, and from the upper end of the hyoid the external rectus. These are clearly the 1st and 3rd myotomes of v. Wijhe, whilst from his 2nd myotome the superior oblique is formed. It follows that, according to v. Wijhe, there are two myotomes (his 3rd and 4th) in the hyoid segment; of which the anterior develops into the external rectus, and the posterior atrophies.

In v. Wijhe's tabular statement it is said that the 7th, 8th and 9th myotomes give rise to the "Vom Schadel zum Schultergurtel ziehende Muskeln nebst dem vordersten Theile des Sternohyoideus." In the text of the paper (quoted above) he states that the sterno-hyoideus develops from the ventral ends of the 9th head- and the most anterior trunk-myotomes, and that it had not been determined whether the 7th and 8th myotomes also grow downwards. It is also to be noted that he does not describe or picture the development of any muscles passing from the skull to the shoulder-girdle. According to Vetter,[1] there is only one such muscle—the trapezius.

The result of my observations is as follows: The embryos were bought from the Laboratory of the British Marine Association at Plymouth. They had been fixed in corrosive sublimate and acetic acid. They were stained in Mayer's acid carmine solution, imbedded in paraffin, and cut into serial sections in transverse and vertical longitudinal planes. The development was followed from Balfour's stage H onwards.

In stage I the pericardium consists of two portions, which are continuous with each other, an anterior or cephalic in the five branchial segments, and a posterior or cervical portion in the neck. The former contains the ventral aorta, the latter the heart (fig. 3A).

The cephalic portion of the pericardium is developed as follows: The formation of the gill-slits does not interrupt the continuity of the head-cavity from segment to segment ventro-lateral to the gut on each side of the head, though it does do so laterally. The pericardium is formed in the 1st and succeed-

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[1] "Kiemen-und Kiefer-muskulatur der Fische," *Jenaische Zeitschrift*, vol. viii., 1874.

ing branchial segments, by approximation of the lower ends of the head-cavity and breaking down of the two splanchnic layers, so that it becomes continuous from side to side across the median line ventral to the gut.   The ventral aorta is formed just above, and indents, the dorsal wall of the pericardium.   A section of the head-cavity extends upwards, on each side, from the upper lateral edge of the pericardium between each two gill-slits, the last being just behind the 4th branchial gill-slit.

The lower end of the cavity in the mandibular segment is continuous with that in the lower end of the hyoid segment, and that again with the pericardium which begins in the 1st branchial segment, but in neither the mandibular nor the hyoid segment does this cavity become continuous with its fellow across the median line ventral to the gut.   These communications between the lower ends of the mandibular, hyoid, and 1st branchial, head-cavities become obliterated by stage K (fig. 7), though the hyoid and mandibular cavities themselves do not disappear until much later.

In the hinder branchial segments the pericardium enlarges by a bulging upward of its upper wall, so that the lower ends of the sections of the head-cavity between the gill-slits no longer join the upper lateral edge, but the outer wall, of the pericardium (figs. 12, 13, 14).   This enlargement is owing to the development and forward bulging of the heart, the auricle of which is now seen in transverse sections of the 4th and 5th branchial segments; whereas previously the heart was confined to the cervical region, and there was only the ventral aorta in the cephalic part of the pericardium (fig 3A).

The cephalic portion of the pericardium is thus in early stages present in all the branchial segments; later on its anterior extremity retreats, so that in stage M it does not exist in the 1st but only in the 2nd and succeeding branchial segments (figs. 20, 21, 22); and finally it appears somewhat suddenly in the 4th branchial segment and is absent in the first three.   This disappearance of the anterior part of the cephalic portion of the pericardium is not due to a collapse of its walls, but to a gradual retreat of its anterior end, owing doubtless to a deficiency in growth relative to that of the rest of the head.

The fate of the sections of the body-cavity extending up-

wards from the pericardium between the gill-slits may now be considered, and they may be taken together, as their development is almost identical in all the five branchial arches.

The upper ends of these branchial head-cavities are a little dorsal to the upper ends of the branchial slits, they pass downwards, and open below into the pericardial cavity (figs. 10–14 and 15–18).

The first change which is apparent is that the walls gradually come together, from above downwards (fig 12), so that the cavity is obliterated, and the inner wall thickens, the outer remaining a single layer of cells. Their lower ends separate from the pericardium by stage N, and they may then be called (provisionally) the branchial muscle-plates. According to Balfour, they are the myotomes of the head, homologous with those of the body; whilst according to v. Wijhe they are visceral plates (Seitenplatte); but a discussion as to their morphological value may best be left until further on.

Immediately after the branchial muscle-plates have separated from the pericardium, their ventral ends are divided off from the remainder of the muscle-plate, and form the coraco-branchiales (figs. 21 and 22) which grow downwards and backwards (fig. 23), until their hind ends become attached to the shoulder-girdle, just outside the insertion of coraco-hyoideus and coraco-mandibularis.

The remainder of the branchial muscle-plate develops into the (branchial portion of the) superficial constrictor, the adductors, interarcuales, and interbranchiales. The three latter series of muscles are formed by ingrowths from the muscle plates, beginning even before they separate from the pericardium (fig. 12). In the 5th branchial segment—where no branchial cartilages are formed—the branchial muscle-plate is converted solely into the superficial constrictor.

Two further changes occur in the superficial constrictor; the dorsal ends grow upward, and become attached to the outer surface of the trunk myotomes (fig. 26), which have by this time overlapped the branchial region dorsally, and the lower ends grow downward, round and outside the ventral longitudinal muscles (i.e. the coraco-mandibularis, coraco-hyoideus, and coraco-branchiales) and meet in the mid-ventral line (fig. 26).

The hyoid section of the head-cavity presents, in stage H, a forward directed upper end (over the top of the hyomandibular gill-cleft), continuous below with a cavity extending down between the hyomandibular and hyobranchial gill-clefts (fig. 1), as described by Balfour.

The anterior part of the upper end begins to be constricted off towards the end of stage H, so that by stage I there are two epithelium-lined cavities lying at the top of the hyoid segment, of which the posterior is continuous with the remainder of the hyoid head-cavity (figs. 2 and 3).

The anterior vesicle then completely separates, and grows forwards and inwards (figs. 5 and 9), and forms, as described by v. Wijhe, the external rectus muscle of the eye.

After the separation of the forepart of its upper end, the inner wall of the hyoid head-cavity thickens, whilst the outer remains a simple layer of cells. The cavity is thus obliterated, from above downwards, and the resulting solid strip of cells is converted into muscles, the upper portion forming the dorsal portion, and the lower the ventral portion, of the hyoid superficial constrictor (figs. 19 and 20). Some of the fibres of the dorsal portion are inserted into the outer surfaces of the hyomandibular and cerato-hyal cartilages (fig. 25). The ventral ends of the lower portions of the hyoid superficial constrictor, i.e. of that below the cerato-hyal cartilages, unite in the mid - ventral line, below the ventral longitudinal muscles (fig. 20).

The mandibular head-cavity is described by Balfour as spatulate in the early stages; there is a dilated upper portion, produced ventrally into a long thin process parallel with and in front of the hyomandibular cleft (figs. 4–7 and 9). This condition lasts until stage M, when the dilated upper end spreads upwards round the eye, its walls collapse, it separates from the remainder of the mandibular cavity, and is converted, as stated by v. Wijhe, into the superior oblique muscle of the eye.

The rest of the mandibular head-cavity undergoes the changes described by Balfour—the cavity is obliterated by the coming together of its walls, of which the inner one thickens. It is converted into three muscles—from above downwards, the

levator maxillæ superioris,[1] the adductor mandibulæ, and the mandibular portion of the superficial constrictor (figs. 24 and 25). The ventral ends of the constrictors of the two sides come together in the mid-ventral line (figs. 24 and 25).

The cervical myotomes follow on in direct series with the brachial muscle plates in stage I. Their position is a dorso-ventral one. From that time onward they begin to overlap the branchial region of the head, both dorsally and ventrally, the shape of the most anterior ones becoming concave with the concavity directed forward. This process continues until, by stage O, the upper end of the 1st cervical myotome becomes attached to the back of the skull (fig. 23). Meanwhile the ventral ends of the first four cervical myotomes have been growing forward lateral to the cephalic portion of the pericardium, and by stage M have extended as far as the level of the 2nd branchial segment (figs. 10-14 and 15-18). By stage N it is found that ventral ends of the first four cervical myotomes have separated off from the upper ends, and that the column of cells so formed has grown still further forwards. Its anterior portion has split longitudinally, the outer slip is attached to the basihyal, and the inner to Meckel's cartilage (figs. 19-21). The hinder end of the column of cells becomes affixed to the coracoid element of the shoulder-girdle. The coraco-mandibularis and coraco-hyoideus are thus formed from the ventral ends of the first four cervical myotomes. Comparison of figs. 10-14, taken from transverse sections with figs. 15-18 from longitudinal sections of the same stage, and figs. 19-23 show that their development has nothing to do with the branchial muscle-plates, or with the retreat of the pericardium from the first three branchial segments.

The shoulder-girdle and trapezius muscle are formed very late in development. The shoulder-girdle is first clearly marked out in stage P, when its upper end is seen to be opposite the junction of the 10th and 11th body myotomes. At the same time the trapezius is first seen—it is formed by delamination of cells from the upper ends of all the cervical myotomes (fig. 27).

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[1] Vetter (*loc. cit.*) describes a muscle—the superior mandibular constrictor—just behind, and having the same origin and insertion as, the levator maxillæ superioris ; but I have not been able to clearly distinguish it from the levator in my sections.

In regard to the morphological relationships of the various muscles of the head, it will be clear from the preceding that the ventral fibres of the superficial constrictor of the hyoid and mandibular segments have no representatives in the branchial region; they are developed from the ventral parts of the hyoid and mandibular head-cavities, from parts which in the branchial region form the pericardium. The lower portions of the superficial constrictor in the branchial region are derived by downgrowth from the branchial muscle-plates. The muscles derived from the branchial muscle-plates are represented, in the hyoid segment by the upper fibres of the constrictor, in the mandibular segment by the levator maxillæ superioris and adductor mandibulæ.

The above description of the development of the muscles of the head of Scyllium has been given without reference to the rival theories of Balfour and v. Wijhe as to their morphological position.

According to Balfour the muscle-plates situated between the gill-clefts are homologous with the muscle-plates of the body, and are somatic structures; whilst v. Wijhe holds that they are splanchnic structures.

V. Wijhe states that there are in stage I myotomes existing above these muscle-plates. Of these he says that there is, in the mandibular segment one, which becomes the superior oblique; in the hyoid segment two, of which the anterior becomes the external rectus, and the posterior atrophies; in the 1st branchial segment one, which atrophies; in the 2nd branchial segment one, which becomes very rudimentary; whilst the myotomes of the 3rd, 4th and 5th branchial segments develop and form the coraco-hyoideus and (according to the table) the trapezius.

Now, (1) it has been shown above that the so-called anterior myotome of the hyoid segment is due to the very early budding of the anterior part of the top of the hyoid head-cavity, to form a vesicle the walls of which become the external rectus. In stage I, at which v. Wijhe's investigations began, there are two cavities, the posterior of which is continuous with the rest of the hyoid head-cavity, but comparison with stage H shows how this has come about. My observations on this point confirm

those of Balfour and Marshall. (2) I can find no trace of any structures which first separate off from the top of the muscle-plates of the hyoid, 1st and 2nd branchial, muscle-plates, and then atrophy or become rudimentary. (3) I have not been able to find evidence of anything in the 3rd, 4th and 5th branchial segments corresponding to the three myotomes stated by v. Wijhe to exist there. All I can see there are the usual muscle-plates, which undergo a development similar to that of the muscle-plates in the 1st and 2nd branchial segments. (4) The trapezius, coraco-mandibularis and coraco-hyoideus are formed from cervical myotomes.

The conclusion is, therefore, that the view of Balfour is the true one—the branchial muscle-plates, and the similarly situated portions of the hyoid and mandibular muscle-plates, are homologous with the myotomes of the body, and are somatic structures.

The superior oblique and external rectus muscles are specialised portions of the mandibular and hyoid myotomes which separate, the former late, the latter very early in development, from the upper ends of their respective myotomes.

The muscles developed from the premandibular segment are probably to be regarded as somatic structures, whilst the ventral portion of the premandibular head-cavity which meets its fellow just above the pituitary involution (and which atrophies as v. Wijhe showed) represents a splanchnic element. This conclusion is supported by consideration of the structure of the iii nerve.

There are thus in the head of Scyllium eight mesoblast segments which develop as shown in the following table.

Segment	1	2	3	4	5	6	7	8
	Premandibular.	Mandibular.	Hyold.	1st branchial.	2nd branchial.	3rd branchial.	4th branchial.	5th branchial.
Somatic	Rect. sup. } i Int. inf. Obliq. inf.	Obliq. sup. iv Levat max. } v sup. Add. mand.	Rect. ext. vi Upper fibres of con-strictor	Constrictor Inter- } ix branchialis Interarcualis Add. arc. viscer.	Constrictor Inter- x branchialis Interarcualis Add. arc. viscer.	Constrictor Inter- x branchialis Interarcualis Add. arc. viscer.	Constrictor Inter- x branchialis Interarcualis Add. arc. viscer.	Constrictor x
				1st Coraco-branchialis	2nd Coraco-branchialis	3rd Coraco-branchialis	4th Coraco-branchialis	
Splanchnic	0	Constrictor v	Lower fibres } vi of con-strictor	0	0	0	0	0

Note.—The Coraco-branchiales are innervated by the 1st and 2nd cervical nerves—(*vide* Vetter, *loc. cit.*).

It follows from the above that the gill-clefts are endoderm pouches projecting to the exterior between the myotomes of the head.

Figs. 28 and 29 are diagrams representing these views—they show how the body-cavity, formed by splitting of the mesoderm plate, develops somewhat differently in the head and trunk, how the myotomes are formed, and how the lessened extent of the body-cavity in the head (*i.e.* the cephalic portion of the pericardium) as compared with that in the trunk may be correlated with the presence of gill-clefts in the former.

A distinction, based on v. Wijhe's work, has been drawn by Ahlborn [1] between a branchiomeric and a mesomeric segmentation in the head. Such a distinction, however, cannot be made, for, as shown above, these segmentations are one and the same.

This distinction, too, of a mesomeric and branchiomeric segmentation in the head, and the absence of somatic elements in the mid region of the head, have been used by Gaskell [2] in favour of his theory of an arthropod ancestry for vertebrates.

The failure of such a distinction, and the presence of somatic muscles in each segment of the head, as shown above, might however be employed as arguments against such a theory.

Some deductions as to the nature of some of the cranial nerves may be drawn from the above. The superior oblique and external rectus eye-muscles are separated and specialised portions of the myotomes of the mandibular and hyoid segments. The nuclei of iv and vi nerves therefore may be regarded as detached portions of the somatic motor nuclei of the v and vii nerves respectively.[3] There is another interesting fact which bears on these genetic relationships. In the dog the somatic muscles innervated by the v and vii nerves (with the possible exception of the anterior digastric) have no posterior root-ganglion fibres.[4] The superior oblique and external rectus muscles, then, in also possessing this peculiarity, resemble the myotomes

[1] "Ueber die Segmentation des Wirbelthierkörpers," *Zeitschrift für Zoologie,* vol. 40, 1884.

[2] *This Journal,* vol. xxxiii., 1899.

[3] This conclusion has already been drawn by Marshall (*loc. cit.*) in the case of the vi nerve, which, he says, may be regarded as an anterior branch of the vii nerve.

[4] *This Journal,* vol. xxxiv.

from which they have sprung. The conclusion that the muscles developed from the premandibular segment are somatic in nature is supported by the facts, that they have no posterior root-ganglion fibres, and that the nerve fibres passing to them have a large maximum diameter—resembling in both particulars the myotomes of the mandibular and hyoid segments.

V. Wijhe based the following laws on his views of the development of the Elasmobranch head-muscles : " Die dorsalen Wurzeln sind nicht nur sensitiv, sondern innerviren auch die aus den Seitenplatten, nicht die aus den Somiten stammenden Muskeln;" and "Die ventralen Wurzeln sind motorisch, innerviren aber auch die Muskeln der Somite, nicht diejenigen der Seitenplatte."

Insomuch, however, as somatic muscles are developed in each segment of the head of Scyllium, it is clear that these laws will not hold. Thus the v, vii, ix and x nerves contain motor fibres to somatic muscles, though having dorsal superficial origins. In this respect Scyllium resembles the Newt and Toad.[1]

On comparison of the muscles developed from head-segments in Elasmobranchs, Amphibia, and Mammals, the chief differences are seen to lie in the development of new splanchnic muscles in all the segments other than the premandibular, and in the disappearance of somatic muscles behind the hyoid segment; and there are correlated changes in the motor nuclei of the hind-brain. This is primarily dependent on different methods of breathing and taking food.

A short comparison may now be made between the development of the head-cavities in Scyllium and Triton.[2]

In following the development of the head-muscles in the Toad and Newt (loc. cit.), I did not investigate the formation of the eye-muscles, and restricted the account to the muscles

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[1] *This Journal*, vol. xxxvi., 1902.

[2] The method employed in numbering the head-segments of the newt and toad (*loc. cit.*), based on a (partly erroneous) conception of v. Wijhe's views, is a wrong one. In these animals there are but 7 mesoblast segments in the head, of which the mandibular is the 2nd ; the difference from Scyllium being that the 5th branchial is absent. As, however, in those papers it was also stated from what gill-arch segment (*e.g.* 1st branchial) each muscle was developed, the difficulty in comparing the results there given with these is not very great.

of the gill-arches. Since seeing what happens in Scyllium, I have
found that a similar development of the eye-muscles takes place
in those animals; but as the evidence I have is not quite con-
clusive, I must postpone giving a description and figures.

The method of formation of the head-cavities, the development
of the cephalic portion of the pericardium, and its
gradual retreat from the anterior branchial segments, the
method of formation and detachment from the pericardium of
the myotomes, are exactly the same in Triton and Scyllium.
Up to the condition shown in fig. 29 the changes are identical.
But from that point development proceeds along diverging
paths, so that the final condition is very different in the two
animals. The details may be readily seen on comparison of
the tabular statement in this paper with that previously given
for the Newt and Toad. One important point of difference may,
however, be considered in detail. In both Scyllium and the
Amphibians there are a lateral and a median series of ventral
longitudinal muscles. In Scyllium the former (*i.e.* the coraco-
branchiales) are derived from head-myotomes, and the latter
(*i.e.* the coraco-mandibularis and coraco-hyoideus) from body-
myotomes. On the other hand, in the Amphibians both series—
the lateral (*i.e.* the longitudinal muscles of the branchial arches)
and the median (*i.e.* the geniohyoid, ventral longitudinal muscles
of the neck and the ventro-lateral muscles of the trunk)—are
developed from head-myotomes.

The development of the head-muscles of Scyllium thus con-
firms the statements made in describing that of the Newt and
Toad. Further, it supports, from the standpoint of compara-
tive anatomy, the views put forward as to the morphological
position of the head-muscles of the dog, and so the truth, for
all the muscles of the head, of Gaskell's generalisation [1] that
the motor fibres of somatic and cross-striped-visceral muscles
have different maximum diameters.

[1] *Jour. of Phys.*, vol. ix.
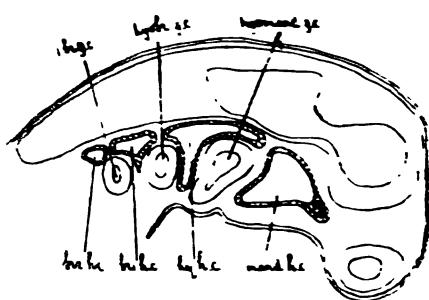
FIG. 1.
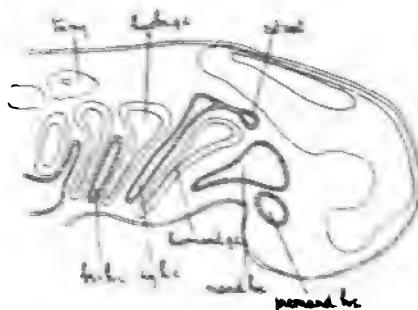
FIG. 2.

FIG. 3.

FIG. 3A.

FIG. 4.

FIG. 5.

MR F. H. EDGEWORTH on Head Muscles in *Scyllium canicula.*
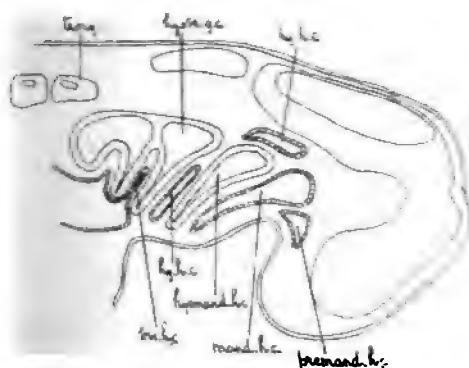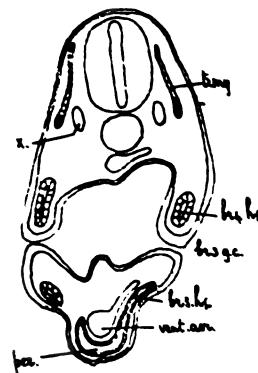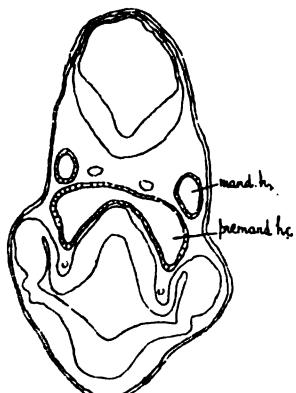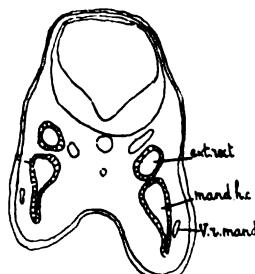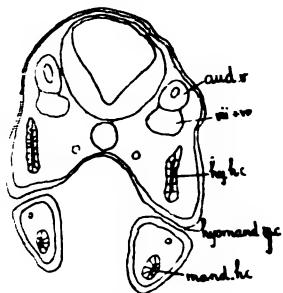
[PLATE V.

FIG. 6.
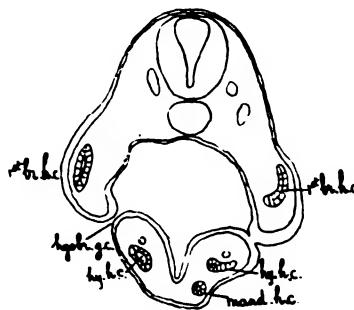
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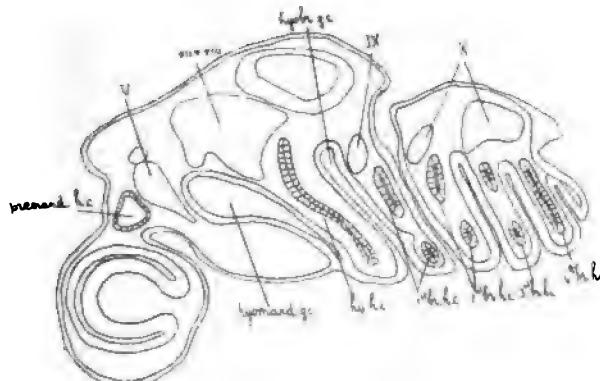
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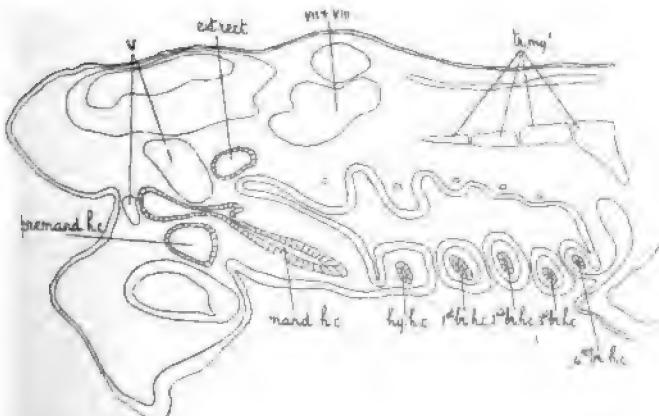
FIG. 9.

MR F. H. EDGEWORTH on Head Muscles in *Scyllium canicula.*
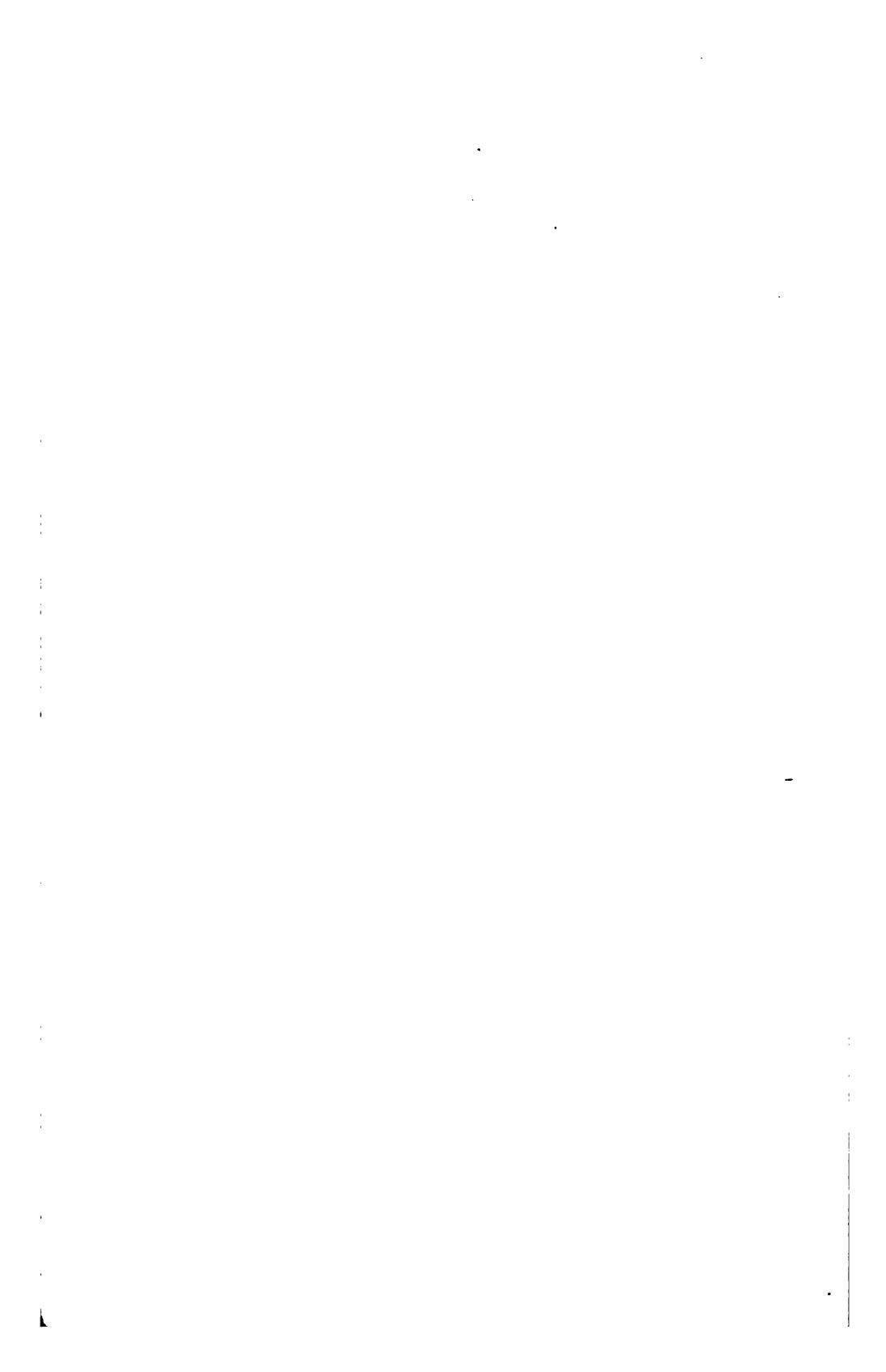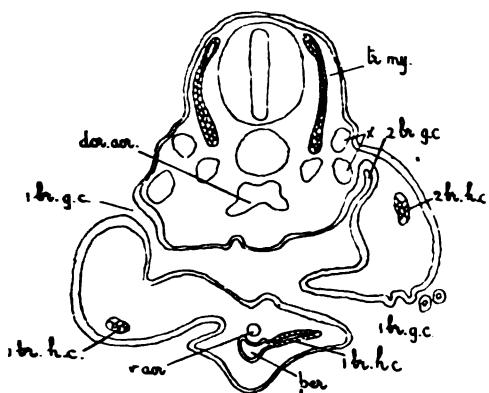
FIG. 10.

FIG. 11.

FIG. 12.

FIG. 13.

FIG. 14.

MR F. H. EDGEWORTH on Head Muscles in *Scyllium canicula.*
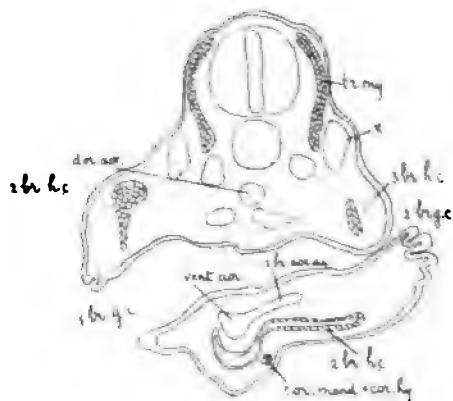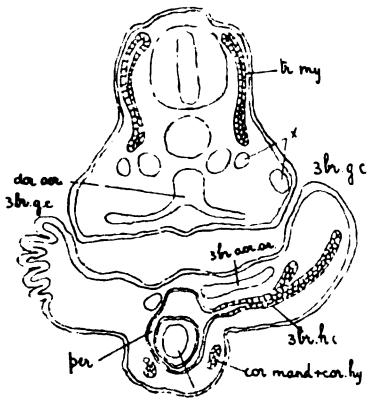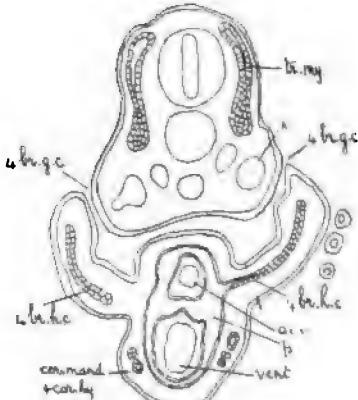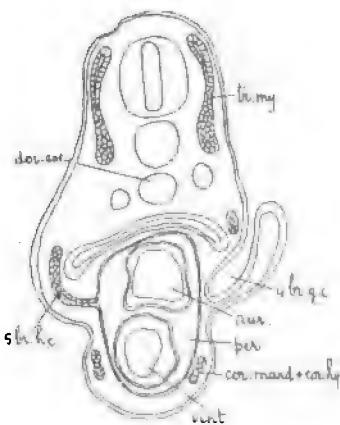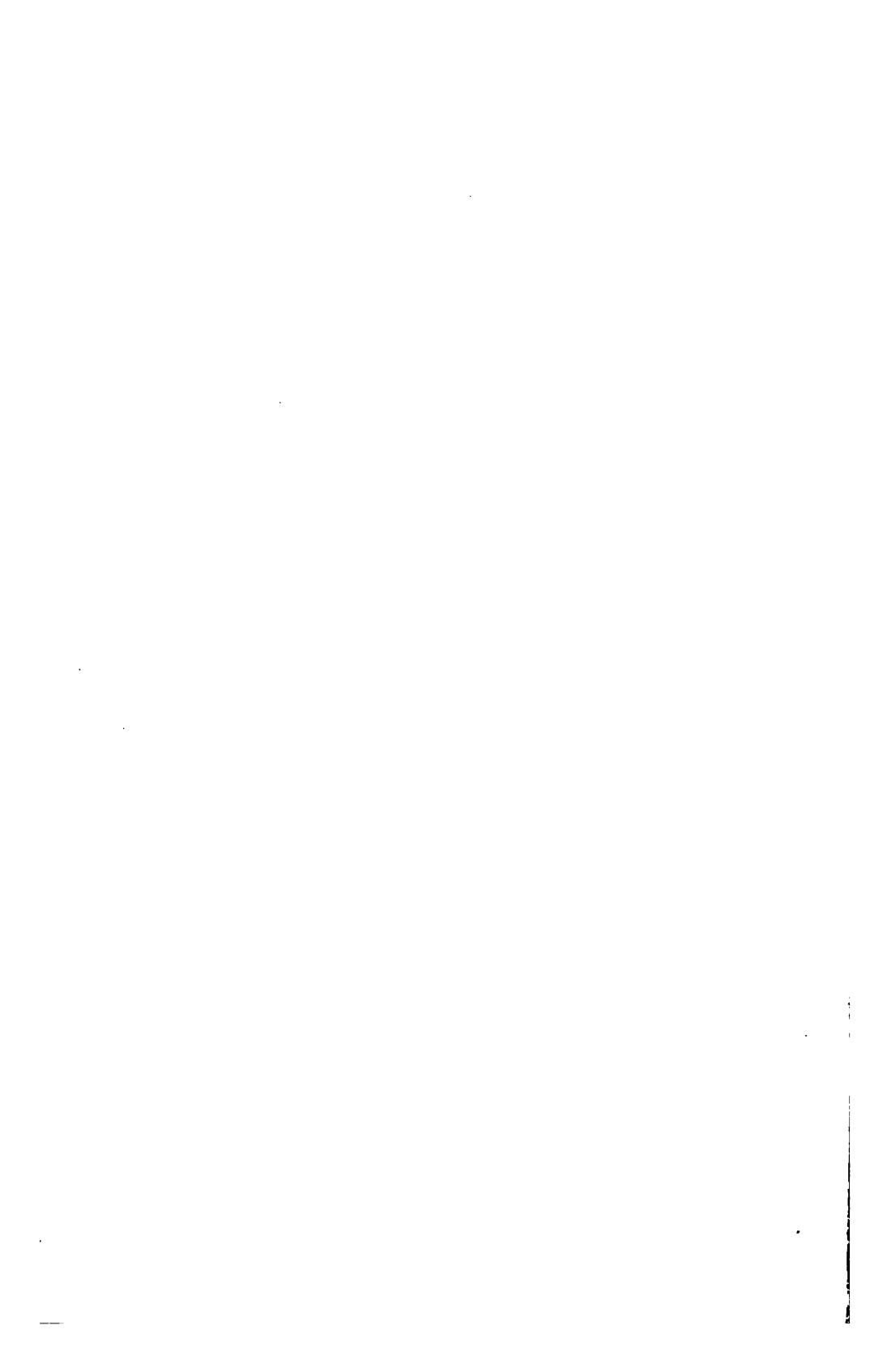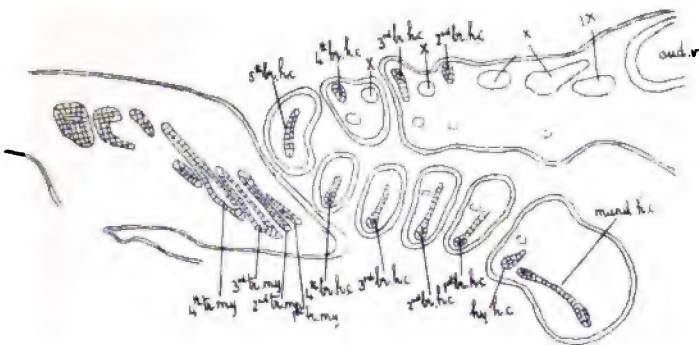
[PLATE VII.

Fig. 15.
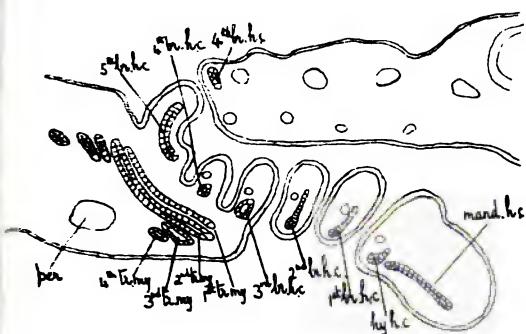
Fig. 16.

Fig. 17.

Fig. 18.

Fig. 19.

Mr F. H. Edgeworth on Head Muscles in *Scyllium canicula*.
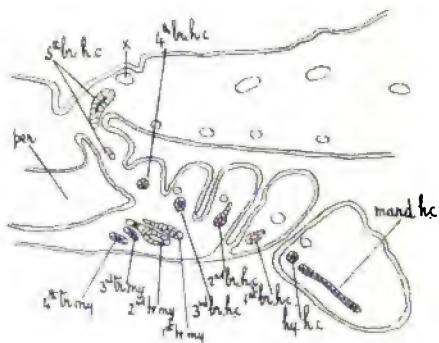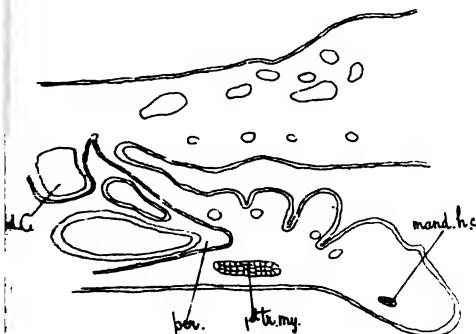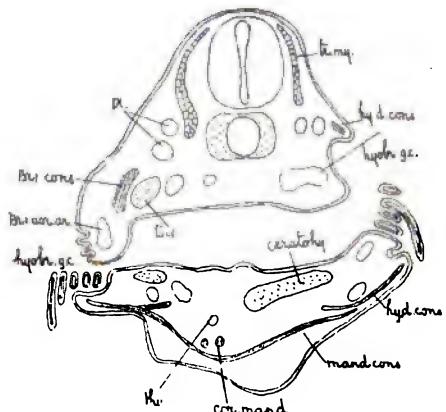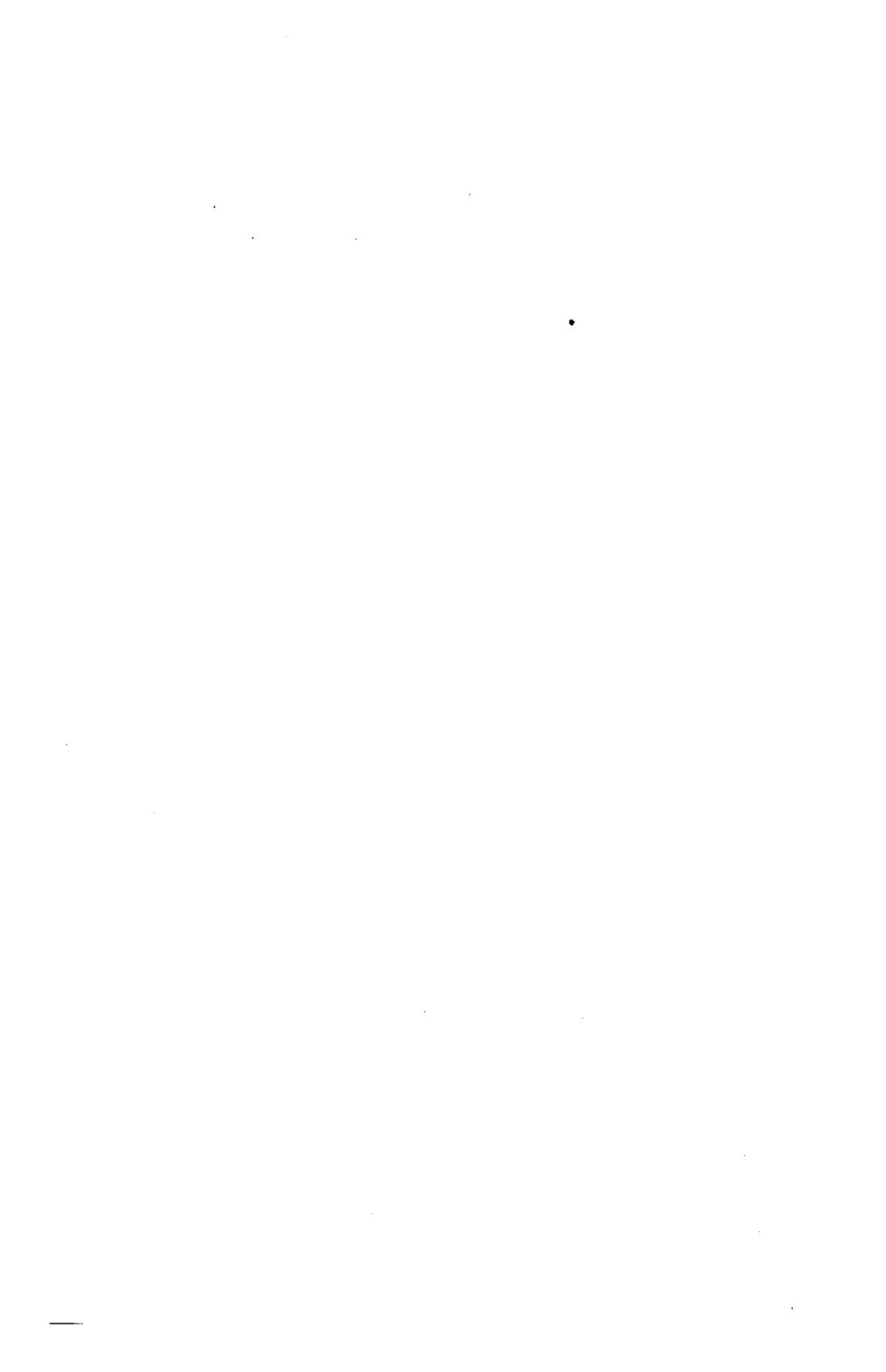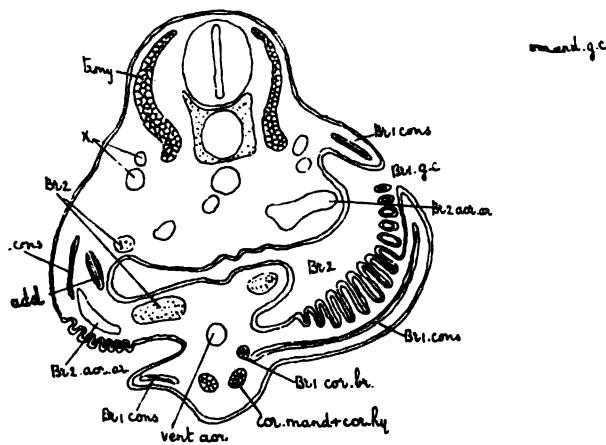
[PLATE IX.

[PLATE VIII.

FIG. 21.

FIG. 23.

Muscles in *Scyllium canicula.*

[PLATE IX.

[PLATE VIII.

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FIG. 21.

and

FIG. 23.

Muscles in *Scyllium canicula*.

[PLATE IX.
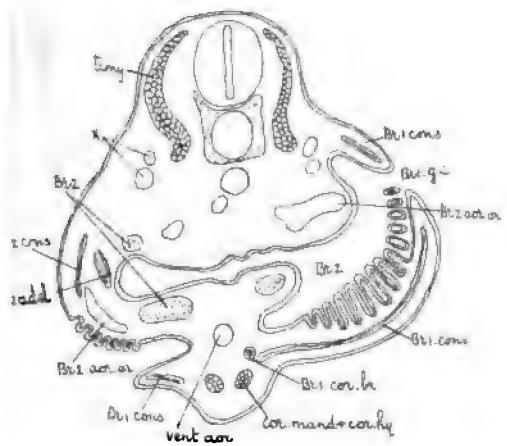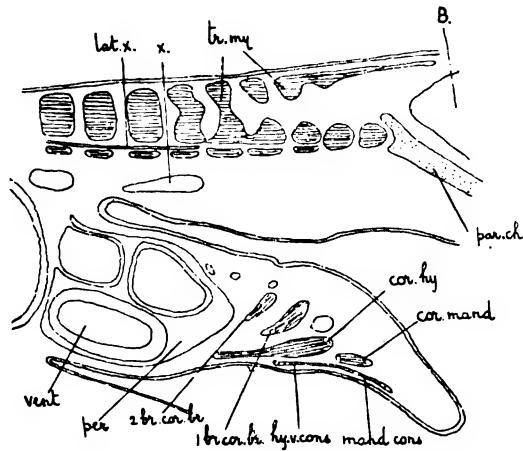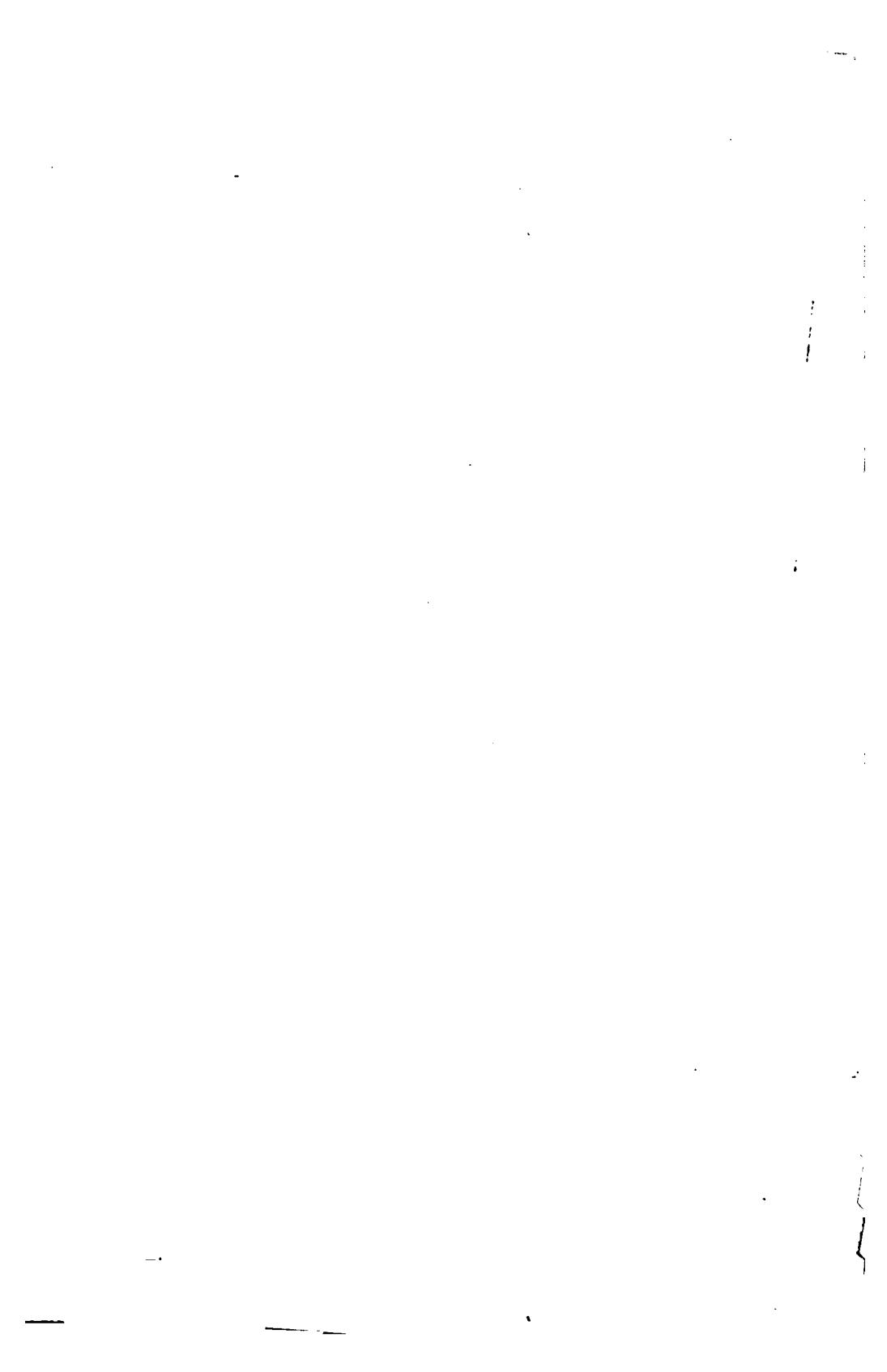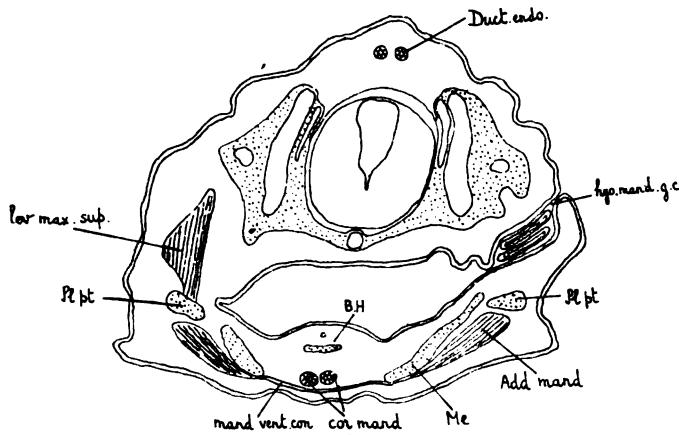
FIG. 24.
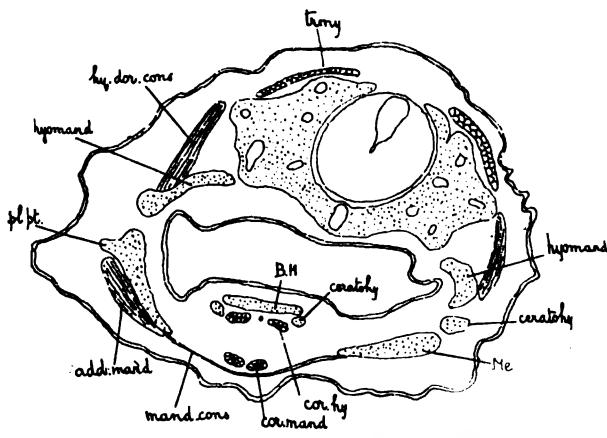
FIG. 25.
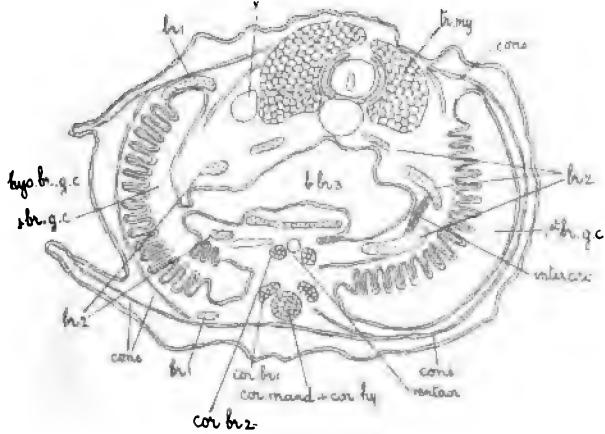
FIG. 26.

MR F. H. EDGEWORTH on Head Muscles in *Scyllium canicula.*
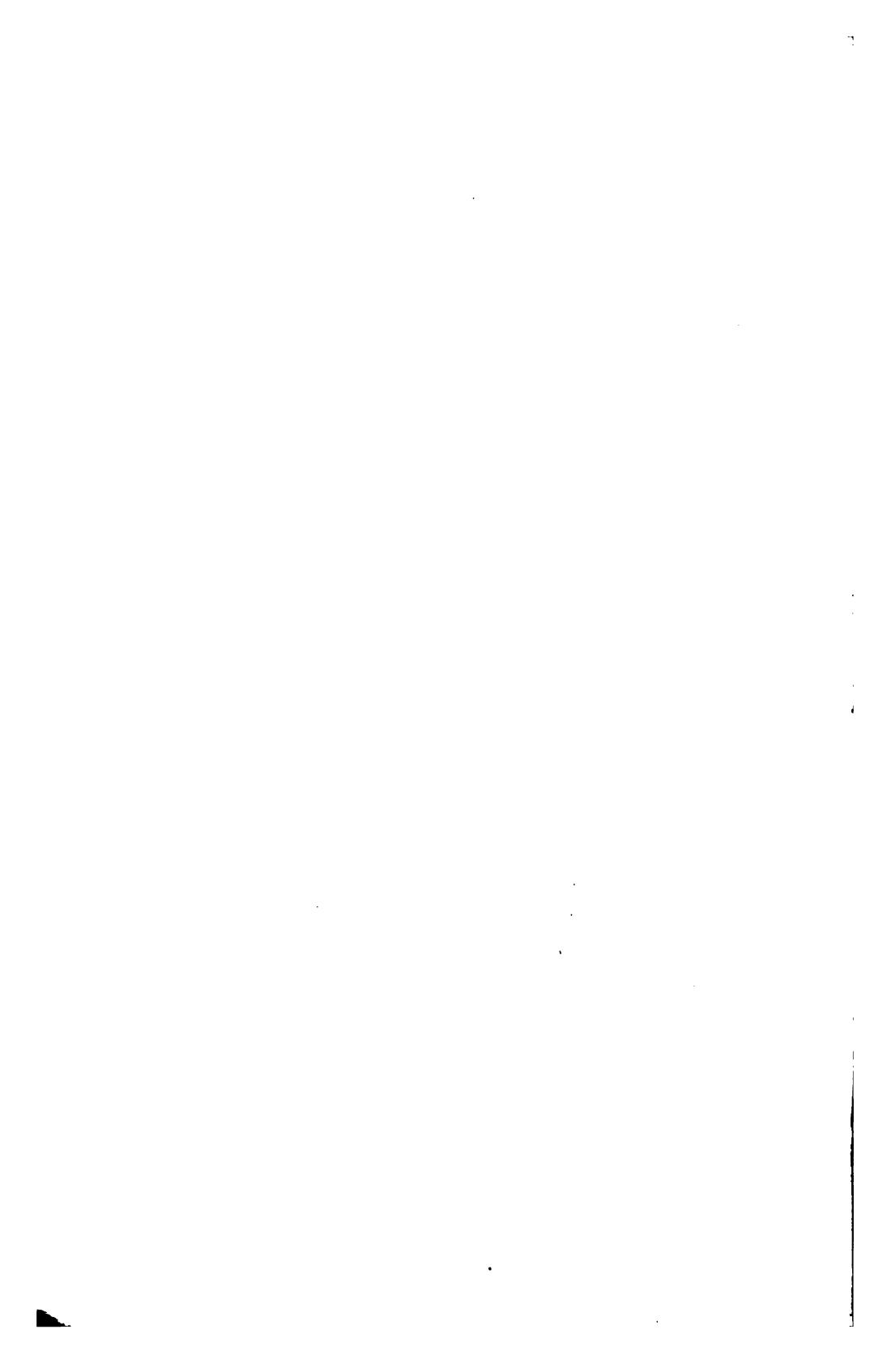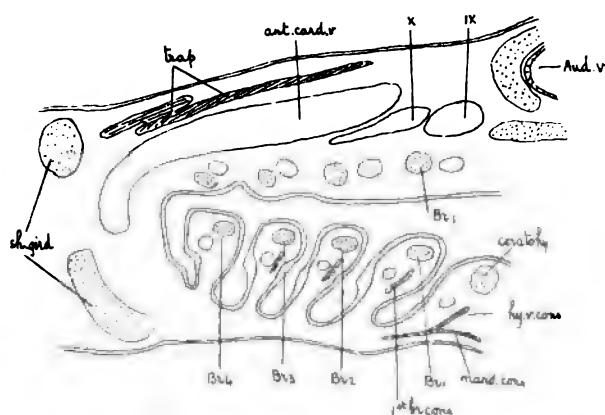
[PLATE X.

Fig. 27.
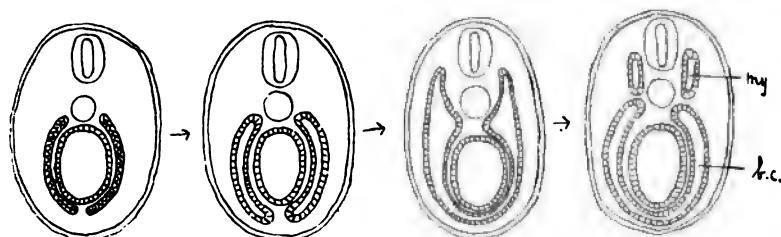
Fig. 28.
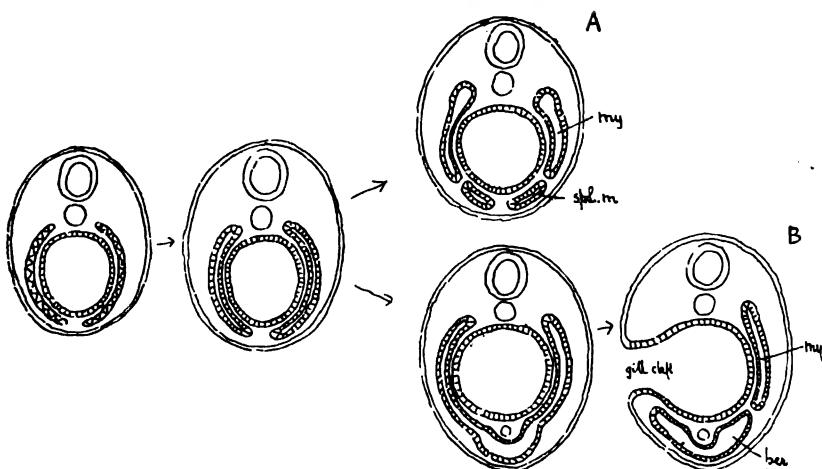
Fig. 29.

MR F. H. EDGEWORTH on Head Muscles in *Scyllium canicula.*
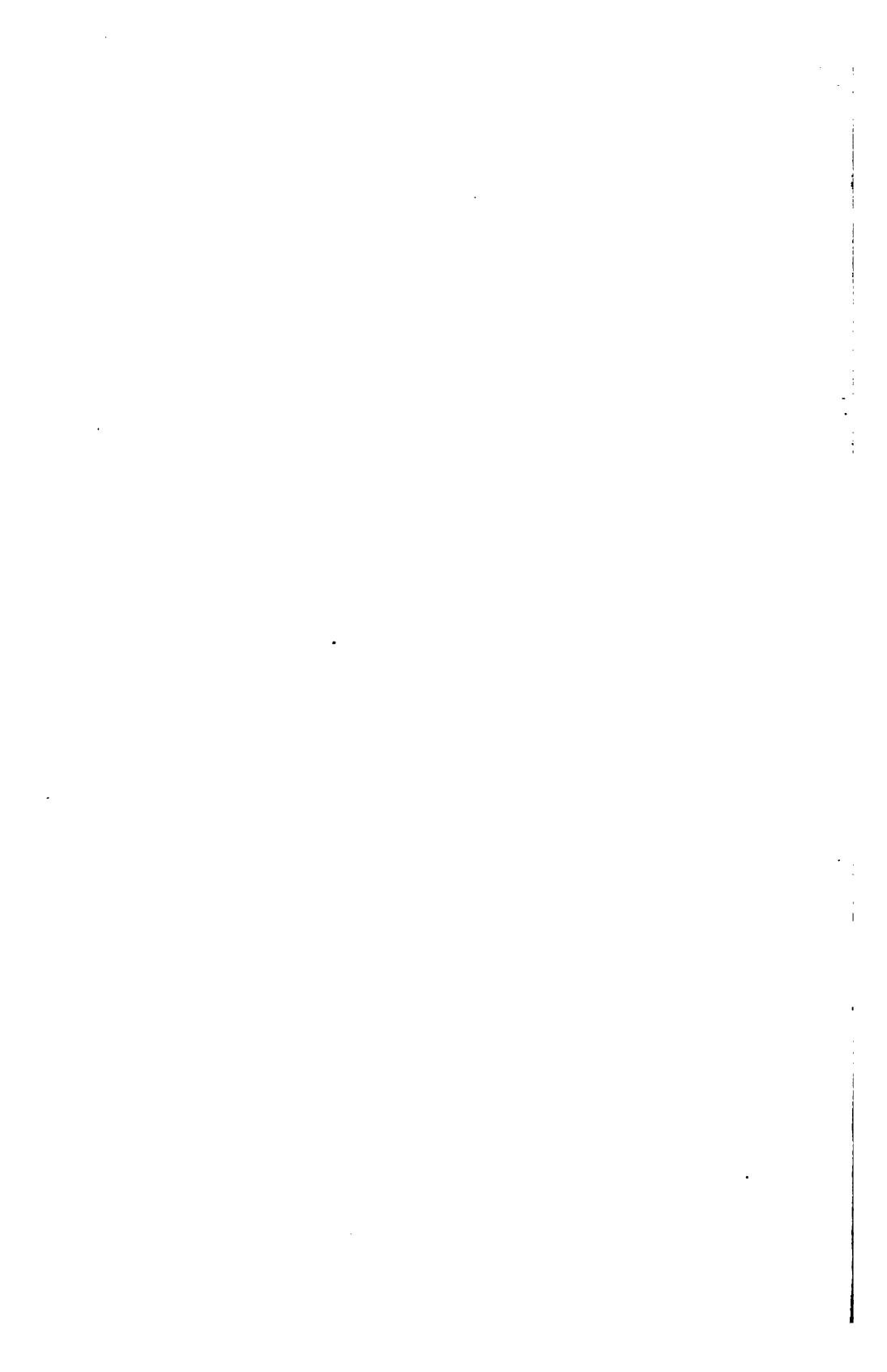
TABLE OF FIGURES. PLATES IV.—X.

Fig. 1. Longitudinal vertical section, stage H.

Figs. 2 and 3. Longitudinal, stage I,—2 is the more external.

Fig. 3A. Transverse section, stage J.

Figs. 4–7. Transverse sections, stage K,—4 is the most anterior ; the left side is a little posterior to the right.

Figs. 8–9. Longitudinal vertical sections, stage K,—8 is the more external.

Figs 10–14. Transverse sections, stage M,—10 is the most anterior ; in 10 and 11 the left side is a little anterior to the right, in 14 the left side is a little posterior to the right.

Figs. 15–18. Longitudinal vertical sections, stage M,—15 is the most external.

Figs. 19–22. Transverse sections, stage N,—19 is the most anterior, the left side is a little posterior to the right.

Fig. 23. Longitudinal vertical section, stage O.

Figs. 24–26. Transverse section, stage P,—24 is the most anterior ; the left side is a little anterior to the right.

Fig. 27. Longitudinal vertical section, stage P.

Fig. 28. Diagrams to show formation of body cavity and myotomes in the trunk.

Fig. 29. Diagrams to show formation of cephalic portion of pericardium and myotomes in the head. A represents the mandibular and hyoid segments, B the branchial segments. In B the left side of the section is supposed to pass intersegmentally to show the gill-cleft.

INDEX.

br.1.cons., 1st branchial superficial constrictor.
br.1.cor.br., 1st branchial coraco-branchialis.
br.1.gc., 1st branchial gill-cleft.
br.1.h.c., 1st branchial head-cavity.
br.interarc., interarcualis.
ceratohy., ceratohyal cartilage.
cons., superficial constrictor.
cor.hy., coraco-hyoideus.
cor.mand., coraco-mandibularis.
cor.mand. and cor.hy., united coraco-mandibularis and -hyoideus.
dor.aor., dorsal aorta.
Duct.endo., ductus endolymphaticus.
hy.h.c., hyoid head-cavity.
hy.d.cons., hyoid dorsal constrictor.
hy.v.cons., hyoid ventral constrictor.
hyobr.g.c., hyobranchial gill-cleft.
hyomand., hyomandibular cartilage.
hyomand.g.c., hyomandibular gill-cleft.
l., liver.
lat.x., lateral line branch of vagus.
lev.max.sup., levator maxillæ superioris.
mand.cons., mandibular constrictor.
mand.h.c., mandibular head-cavity.
Me., Meckel's cartilage.
my., myotome.
par.ch., parachordal cartilage.
per., cephalic portion of pericardium.
pl.pt., palato-pterygoid bar.
premand.hc., premandibular head-cavity.
sh.gird., shoulder-girdle.
spl.m., splanchnic muscle.
thy., thyroid gland.
trap., trapezius
tr.my., myotome of trunk.
vent., ventricle of heart.
vent.aor., ventral aorta.
V.e.mand., mandibular branch of v nerve.

THE SKELETON OF A NATIVE AUSTRALIAN. By W. H. BROAD, M.B., Ch.B., *Robert Gee Fellow in Anatomy, University College, Liverpool.*

THE following is a description of an Australian skeleton presented to the Anatomical Museum of University College, Liverpool, by Mr C. H. Robinson.

Nothing is known regarding the source of the skeleton, nor the particular tribe to which it belonged.

The bones are small and slender, but well formed. They are probably those of an aged female about 4 ft. 6 ins. in height.

In this description considerable help has been derived from the "Challenger" Reports of Sir William Turner (1), whose methods for obtaining the various indices and measurements have been followed.

VERTEBRAL COLUMN.

Vertebral formula C_7 T_{12} L_5 S_5 Co. (?).

The *Cervical Vertebræ* are small but well formed. Excepting the first, sixth, and seventh, the spinous processes are strongly bifid.

The *Thoracic Vertebræ* are normal, except that the ninth articulates with the heads of two ribs.

The *Lumbar Vertebræ* all show well-marked mammillary processes, and except the first, exhibit traces of an accessory process.

The lumbar indices are :—

$$
\begin{array}{ll}
L_1 & 120 \\
L_2 & 113\cdot3 \\
L_3 & 109\cdot5 \\
L_4 & 109\cdot1 \\
L_5 & 90\cdot1 \\
\end{array}
$$

The *lumbo-vertebral* index is 106·4. The average lumbo-vertebral index amongst Australians is 107·8 (Cunningham) (3). This index, which is the relation of the sum of the anterior measurements of the lumbar bodies to the sum of the posterior measurements, has an important bearing on the *lumbar curve*.

Professor Cunningham (3) in his paper on the Lumbar Curve shows that a *high* lumbo-vertebral index is characteristic of the lower races and also of the higher apes.

The following table is taken from the above-mentioned paper :—

LUMBO-VERTEBRAL INDICES.

Man {
European   95·8
Negro   105·4
Bushman   106·6
Australian   107·8
}

Apes {
Semnopithecus 105·1
Gibbon   107·1
Gorilla   108·1
}

In Europeans *all* the bodies of the lumbar vertebræ, except usually the first, have an index below 100, *i.e.* are longer anteriorly than posteriorly, and consequently have a *lumbo-vertebral index* of less than 100.

In the skeleton under consideration, the *fifth lumbar* vertebra is the only one with an index below 100, and the lumbo-vertebral index is 106·4.

FIG. 1.—Sacrum of Aboriginal Australian—(⅔ nat. size).

The *Sacrum* is a small bone measuring 105 mm. in length and 98 mm. in breadth. (Average Australian length 106 mm., breadth 100 mm.—Turner (1).

The neural canal is roofless except opposite the third and fourth

vertebræ, which possess rudimentary spines. There are three well-marked depressions on the first three vertebræ for ligamentous attachment, of which the first is the deepest.

The first, second, and a small part of the third vertebræ form the auricular surface, which is notched a little below its middle.

Sacral Curve.—The anterior surface of the sacrum shows a remarkably shallow curve. The greatest depth of this concavity is opposite the body of the third sacral vertebra, and measures 11 mm.
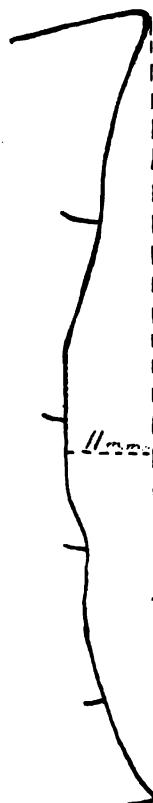
Fig. 2.—Sacral Curve in Aboriginal Australian—(nat. size).

The average maximum depth in Australian sacra is 16·1 mm. (Paterson) (2).

The curve is more marked *below* than above the deepest point.

Sacral index.—The sacral index is 93·4 (dolichohieric).

In Sir W. Turner's tables the Australian sacral index (eight cases) varies from 93 in the Perth tribe to 104 in the Riverina Australian.

In Professor Paterson's table (eight cases) the average is 106.

Obviously the sacral index must always vary with the curvature, and in this case a low index and a shallow curve are associated together.

The *Innominate Bones* are small, and the expanded ilia, triangular thyroid foramina, and everted lips of the pubic arches clearly demonstrate female characteristics. Muscular impressions are poorly marked, *e.g.* the curved lines, and the ilio-pectineal eminences are exceedingly slight and smooth.

The thyroid foramen is triangular, and the vertical diameter of the foramen exceeds the transverse,—a female characteristic (Turner). The cotyloid notch of the acetabulum is unusually wide.

Indices of the Innominate Bones.

								Australians (Turner).			
1. Innominate index	...	R.	73	L.	72	...	from	76	to	83
2. Iliac index	...	R.	105	L.	111	...	,,	123	,,	137
3. Ischio-innominate index		R.	31	L.	29	...	,,	40	,,	46
4. Pubo-innominate index		R.	51	L.	50	...	,,	40	,,	48

It will be seen that in the first three of the above indices these innominate bones are considerably below the Australian standard as given in Sir W. Turner's tables. This is accounted for by the fact that the bones possess an unusually *long* and *narrow* ilium.

At the same time the *pubo-innominate* index is *above* the standard.

Now the pubo-innominate index shows the relation of the os pubis to the breadth of the innominate bone, so that in this case the pubis contributes more than is usual to the width of the os innominatum.

Femur.—*Maximum length*, R. 372 mm., L. 375 mm. (Average Australian 452 mm. [Turner].)

Maximum trochanteric length, R. 362 mm., L. 364 mm.

The difference between the maximum length and the maximum trochanteric length determines the amount of obliquity of the neck.

In the present instance the difference amounts to 10 and 11 mm. respectively, showing an *increase* in the angle over the normal.

The shaft of the femur is slender, and exhibits only slight muscular

impressions. It also shows the characteristics of Broca's 'femur à colonne.'

A feeble *trochanter tertius* is present on the left femur, and the right gluteal ridge is prominent.

The upper part of the shaft is flattened from before backwards and bulges outwards, a character noted by Sir W. Turner both in Australians and New Zealanders. The shaft presents a marked convexity forwards and is somewhat twisted outwards. The spiral line is absent, but in a situation corresponding to the position of its upper end there is a prominent tubercle. On the upper surface of the posterior portion of the internal condyle there is a well-marked articular facet (6). This will be referred to later.

The popliteal surface is slightly convex from side to side.

Popliteal indices, R. 92, L. 96. (Average Australian index 94,—Hepburn) (7).

Tibia.—Length, R. 312, L. 310. (Average 375 mm.,—Turner.)

This slight inequality in length compensates for the unequal length of the femora.

The tibia is platyknemic; the head is placed obliquely, the articular surfaces looking upward and backward; the external articular surface is convex from before backwards; and on the anterior surface of the inferior extremity there is an articular facet (5), continuous with the inferior articular surface, which articulates with the astragalus.

$$\text{The } \textit{Tibio-femoral index} \left(\frac{\text{length of tibia} \times 100}{\text{length of femur}} \right)$$

is R. 83, L. 82.

These indices correspond with the mean of six Australians measured by Sir W. Turner, which was 82·9.

He places the Australians amongst the *dolichoknemic*, or long-legged series.

The height of an individual equals twice the combined length of the femur and tibia (Turner). In the present instance that would be F. 372 + T. 312 = 684 × 2 = 1368 mm., or about 4 ft. 6 ins. This is considerably below the average height—5 ft. 5 ins.—assigned to Australian races in the tables of racial stature (8).

Fibula.—Length, R. 303 mm., L. 302 mm. The fibula is small, slender, flattened from side to side, and presents a convexity inwards and forwards.

There is a large surface for the attachment of the tibialis posticus.

UPPER LIMB.

Clavicle.—Length, R. 110 mm., L. 108 mm. (Average 142 mm.)

The surfaces are smooth, muscular attachments being feebly

developed, whilst ligamentous impressions are well marked.   The subclavian groove is absent.

Scapula.—Length, R. 108 mm., L. 112 mm.   Breadth, R. 76 mm., L. 78 mm.   (Turner's average Australian, length 150 mm., breadth 100 mm.)

Scapular index, R. 70, L. 69·5.   (Average 66.)   The scapula is long and narrow, and the suprascapular notch is absent.

Humerus.—Length, R. 266 mm., L. 256 mm.   (Average 300 mm.) Sir W. Turner's Australians, with one or two exceptions, had the right humerus slightly longer than the left.   He mentions an unusually large disparity between the length of the right and left humeri of an Australian female, which amounted—as in this case—to 10 mm.   The musculo-spiral groove is absent, the radial depression is well marked.

Radius.—Length, R. 200 mm., L. 198 mm.   The pronator impressions are well marked.   The lower extremity is bent forwards considerably.

$$Radio\text{-}humeral\ index = \frac{length\ of\ radius \times 100}{length\ of\ humerus} = R.\ 75,\ L.\ 76.$$

These correspond with the mean given by Sir W. Turner, which is 76 (mesatikerkic).

The average European index is 72·4 (brachykerkic).

Ulna.—Length, R. 220 mm., L. 219 mm.   The greater sigmoid cavity is peculiar, being directed mainly outwards, and only slightly forwards.   The lesser sigmoid notch is absent, the side of the radial head articulating with the lower and external portion of the greater notch.

The habitual attitude would appear to have been one of semiflexion and semipronation of the forearm.

$$Intermembral\ index\ =\ \left\{ \frac{(humerus + radius) \times 100}{femur + tibia} \right\}\ =$$

R. 68·1, L. 68·6.

The indices in Sir W. Turner's Australians varied from 67·4 to 72.

SKULL.

The *measurements* compared with those of Australian skulls from the tables of Sir W. Turner and Topinard (4) :—

				Turner.	Topinard.
Antero-posterior diameter	...	166 mm.	...	173–192	
Transverse	„	... 122	„	... 122–135	
Vertical	„	... 130	„	...	
Cephalic index	...	... 73·4		... 68–72	71·4
Vertical „	...	... 77·1		... 65–72	

					Turner.	Topinard.
Facial index	...	...	65·2	...	...	56·6
Nasal „	...	...	57·1	...	50–56	53·3
Orbital „	...	...	84·4	...	72–84	80·4

Capacity (millet seed) ...   1141·6 c.c. ...   998–1330 1181 F.
                                                            1347 M.

The skull is dolichocephalic, microcephalic, prognathous, and platyrrhine.

It is, however, of larger capacity and less dolichocephalic than usual amongst Australians. Viewed from in front, the cranium has a 'keel-shaped' appearance.

Teeth.—Dentition is complete. The molars are worn and flattened, and several teeth in the upper jaw are carious.

The lower jaw is a small but thick and powerful bone; the rami are short and broad, and the genial tubercles prominent.

Summary.—The chief points of interest about the skeleton and skull are—

1. The small size of the bones.

2. The shallow sacral curve, and the notched auricular surfaces.

3. A narrow ilium associated with a long and narrow os pubis.

4. The characteristics of the bones of the lower limbs, peculiar to those races accustomed to the "squatting" posture, described by Thomson and Charles.

These are—a facet on the upper and posterior surface of the internal condyle of the femur; the obliquely placed tibial head; the convexity from before backwards of the external condylar surface of the head of the tibia; the facets on the anterior inferior surface of the tibia, and on the upper surface of the neck of the astragalus; the large surfaces for attachment of the tibialis posticus on the tibia and fibula.

5. The curious formation of the articular surfaces forming the elbow and superior radio-ulnar joints.

6. The microcephalic, dolichocephalic, platyrrhine and prognathous character of the skull.

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(2) *Scientific Transactions of the Royal Dublin Society*, vol. v.,—"The Human Sacrum."—Prof. A. M. PATERSON, M.D.

(3) Royal Irish Academy,—*Cunningham Memoirs*—"The Lumbar Curve in Man and Apes."—Prof. D. J. CUNNINGHAM, M.D., F.R.S.

(4) "Anthropology."—Dr P. TOPINARD.

(5) *Journal of Anatomy and Physiology* (vols. xxiii. and xxiv.)—"The influence of posture on the form of articular surfaces of the tibia and astragalus in different races of man and the higher apes."—ARTHUR THOMSON, M.A., M.B., &c.

(6) *Journal of Anatomy and Physiology* (vol. xxviii.)—"The Panjabi and Squatting."—Prof. R. HAVELOCK CHARLES.

(7) *Journal of Anatomy and Physiology* (vol. xxxi.)—"The Trinil Femur, contrasted with the femora of various savage and civilised tribes."—Dr HEPBURN.

(8) *Transactions of Anthropometrical Committee, British Association.*

ARE THE CRANIAL CONTENTS DISPLACED AND THE BRAIN DAMAGED BY FREEZING THE ENTIRE HEAD? By JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's College, Belfast.* (PLATE XI.)

AMONGST the methods employed in the investigation of the topographical relations of the various organs of the body, that of making sawn sections of the frozen subject has been used very extensively and with great advantage. It is true that this plan has been, of late years, superseded to a large extent owing to the discovery of the valuable properties of formol as a hardening and fixing agent. There are still, however, various purposes for which no other method gives such satisfactory results as freezing. This is particularly the case when we wish to obtain a connected and continuous view of the structures situated in a series of parallel planes passing through large portions of the body, such, for instance, as a number of sagittal sections of the trunk. In regions where the structures lying in a particular plane vary very considerably in density and degree of fixation, sections made with a saw after freezing the parts give better results than sections made, partly with a knife and partly with a saw, after hardening in formol.

This is particularly the case with the head where the osseous tissue is so considerable and irregular in outline that it is necessary to use the saw for the soft tissues as well as the bones, although not only the non-osseous structures, but also the bones in places like the walls of the nose and in the tympanum, do not cut well with a saw after simply hardening them in formol.

In some recent observations on cranio-cerebral topography where I desired to obtain the relations of the deep parts of the

brain to the surface, frozen sections of the entire head afforded,
so far as I was able to judge, reliable and trustworthy data.
The utility of this method has been called in question by
Professor August Froriep,[1] who, from an examination of published
drawings of such sections, as well as from his own experiments,
has come to the conclusion that during the freezing process the
brain suffers such serious injury and disturbance of its parts as
to greatly impair the value of any deductions drawn from a
study of sections obtained by this method of fixation. Froriep
holds that the displacement of a portion of the skull contents is
a normal concomitant of the freezing of the unopened head, and
it must be admitted that the anatomical relations of the skull
and brain and the changes in volume associated with the freezing
process suggest the probability of such an occurrence.

We may regard the cranium as a box with rigid walls having
only one aperture (the foramen magnum) of any appreciable
size, and through which some of the cranial contents might be
forced. All the other cranial openings are not only much
smaller, but they are practically closed by nerves or other
structures. The contents of this box are the brain, which is a
large organ of soft consistence, and a variable amount of free
fluid situated between the skull and the brain, or in the ventricles
of the latter organ. Froriep draws attention to the fact that
79 p.c. of the brain weight is estimated to consist of water, and
consequently a brain weighing 1300 grammes would contain
1027 grammes of water. The free fluid in the cranial cavity
may be taken as from 50 to 100 grammes, and we may accordingly
estimate the amount of water in the cranial cavity as 1100
grammes. Water expands when frozen in the proportion of 1
to 1·09, so that the mass displaced from the cranial cavity during
the freezing of an unopened head ought to be 99 grammes. In
a female subject aged 39 years Froriep calculated that the mass
actually expelled from the cranial cavity during the freezing of
the head amounted to 30 grammes or less than $\frac{1}{3}$ of the amount
that might theoretically be expected. From Froriep's account
of this experiment it would appear that the mass protruded was

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[1] "Ueber ein für die Lagebestimmung des Hirnstammes im Schädel verhäng-
nissvolles Artefact beim Gefrieren des menschlichen Cadavers," *Anatomischer
Anzeiger*, Bd. xix., 1901.

unusually large, and certainly there is no experimental evidence to support the view that the expansion of the brain during the freezing process is equal to what it would be if the 79 p.c. of water in its composition behaved as ordinary water.   This water is probably in intimate chemical union with other substances, and the resulting compounds may act in a very different manner from water as regards change of volume during the freezing process.   Further, even in the case of the free water the substances it holds in solution may influence its change of volume when frozen.   In the present state of our knowledge we are not justified in assuming that the water in the cranial cavity will expand as ordinary water does when frozen, and consequently any objections to the use of the freezing method in the study of cranio-cerebral topography based on such a supposition must not be admitted without experimental proof.

   Froriep holds that his view is supported by the results of a critical examination of the various illustrations that have been published of frozen sections of the entire head.   He first selects Pirogoff's Atlas,[1] and mentions a number of plates in this work showing alterations in form and displacements of various parts of the brain which Froriep believes were due to the freezing process.   One of these plates has been reproduced (fig. 2) in Froriep's paper.   He considers that this figure illustrates the artificial distortion of the basal portions of the brain, which, however, had been dammed up below by the early freezing of the cervical part of the contents of the spinal canal. If the drawing were a correct representation of the appearance of the section, I should be willing to agree with Froriep's interpretation, but it seems to me that Pirogoff's plates are so diagrammatic and inaccurate that they ought not to be accepted as satisfactory proofs of the existence of such deformities.   In the figure of a median section of the head which Froriep has reproduced from Pirogoff, the upper four cervical vertebræ are shown with the upper part of the larynx.   I assume from its position that the larynx is represented, but it needs a vivid imagination to recognise the epiglottis or the superior laryngeal aperture, and it will hardly be maintained that the freezing

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[1] *Anatome topographica sectionibus per corpus humanum congelatum triplici directione ductis illustrata*, Petropoli, 1859.

process had altered almost beyond recognition these parts of the larynx. When the larynx is so badly figured, what reliance can be placed upon the drawings of the brain ?

Professor Froriep next refers to Braune's Atlas,[1] and selects Pl. I. and II. which were prepared from median sections of the bodies of a male and a female subject. He admits that these drawings give essentially correct pictures of the medulla, pons and cerebellum free from the characteristic signs of distortion due to freezing, but the diameter of the medulla and spinal cord is too great. Froriep enquires how Braune succeeded in obtaining correct pictures from frozen sections, and believes that the following extract from the text to Pl. I. shows how this was accomplished :—" Besondere Mühe erforderte es, die einzelnen Teile des Gehirns deutlich zur Anschauung zu bringen. Es mussten Durchschnitte an frischen Gehirnen dazu dienen, die Zeichnung innerhalb der schon festgestellten Contouren sauber und deutlich zu machen." In fig. 3 Froriep gives a copy of the upper part of Pl. C of Braune's Supplement[2] to his large atlas as an illustration of what he considers to be the usual appearance of a frozen median section of the head. With reference to the two plates in Braune's *Topographisch-anatom-ischer Atlas*, I do not think that the text or the appearance of these plates justify the assumption that Braune corrected the outline of the various parts of the brain to make them conform to what his anatomical instincts conceived to be their normal position. The special purpose of the publication of the plates in the "Supplement," was to show the position of the pregnant uterus and its contents, and it is evident that no attempt was made to give an accurate drawing of the brain or spinal cord.

When a frozen section is made, particularly such a large one as a median cut through the entire body, the heat produced by the friction of the saw causes a partial thawing of the surface, and any cavities normally occupied by fluid are apt to become filled up near the surface of the section with sawdust, and after the section is made the exposed surfaces are covered by a

[1] *Topographisch-anatomischer Atlas.* "Nach Durchschnitten an gefrorenen Cadavern." Leipzig, 1888.

[2] " Die Lage des Uterus und Fœtus am Ende der Schwangerschaft. Nach Durchschnitten an gefrorenen Cadavern." *Supplement zu dem topographisch-anatomischen Atlas des Verfassers*, Leipzig, 1872.

more or less thick layer of this dust.   In order to define clearly
the different structures, it is necessary to wash the surfaces with
water and even to scrub them with a nail-brush. ·If this be
done rapidly the surface becomes frozen again in a few
minutes.   In the case of the brain and spinal cord, the spaces
usually occupied by the cerebro-spinal fluid are found to contain
more or less of this sawdust-looking material.   In such sections
as those of Braune's the spinal cord is represented as too large ;
this I thought was due to the subarachnoid spaces being occupied
by this dust, which presents a considerable resemblance to the
naked-eye appearance of a sawn section of a frozen cord.   As we
shall afterwards see, Froriep gives an entirely different explana-
tion of the origin of this material.

In his description of a median section of a pregnant woman,
Waldeyer [1] refers to the imperfect preservation of certain parts
of the brain, and he attributes this to the fact that the body had
been kept for several days during warm weather before being
placed in the freezing mixture.   Froriep considers that the
appearances of this brain suggest that it had suffered the usual
changes associated with the freezing process, but he admits that
the liability to post-mortem changes increases the difficulty of
determining the real cause of the damaged appearance of the
brain which may be seen in frozen sections.

Froriep does not mention Macewen's *Atlas of Head Sections*
published in 1893, although it contains a more extensive series
of illustrations of frozen sections of the entire head than any
other atlas.   This work contains 53 photogravures made from
photographic plates of frozen sections of 7 subjects.   The first
13 plates contain a series of coronal sections of the head
of a man aged 60 years.   The brain was evidently in a good
state of preservation before being frozen, and I do not think the
sections show any appreciable signs of displacement and injury
to the brain such as Froriep regards as of normal occurrence.
Some of the other series of sections appear to me to indicate
that the subjects had not been obtained with the brain in a well-
preserved condition.   In some places the distinction between
the white and grey matter is not well marked, while in others
the brain had shrunk so as to have an abnormally large space

[1] *Medianschnitt einer Hochschwangeren bei Steisslage des Fœtus*, Bonn, 1886.· ·

between its surface and the cranial wall. In none of them am
I able to detect signs of abnormal expansion of this organ.

According to Froriep, Pl. I. and II. in my work on *The
Topographical Anatomy of the Child* show, on careful examina-
tion, evidence of displacement of certain parts of the brain due
to the freezing. These plates represent median sections through
the entire trunk of a girl 13 years old and of a boy 6 years old.
Froriep states that they demonstrate that the mid-brain and
the vermiform process had been depressed by the freezing, but
he does not give any reasons for this opinion. He also considers
that the optic commissure had been displaced, and, in support of
this view, refers to the fact that it is shown lying above the
dorsum sellæ. At the time when these sections were made, the
optic commissure was described as lying against the optic groove
of the sphenoid bone, and I must admit that although both my
plates show it at a considerable distance from that groove, I did
not detect the discrepancy. Since then this error in our text-
book anatomy has been exposed. Thus, Lawrence[1] found, on
careful dissection, that in a girl $4\frac{1}{2}$ years old the commissure
was placed far back from the optic groove and olivary eminence,
so that a large part of the upper surface of the pituitary body
was visible in front of it; and in a man the commissure almost
entirely covered the pituitary fossa, and its anterior border very
nearly corresponded with the posterior border of the olivary
eminence, but did not touch the latter, and, as in the girl, was
quite removed from the optic groove. According to Zander,[2] the
length of the intra-cranial portion of the optic nerve ranges from
6 to 21 mm.; if that be so it is evident that the position of
the optic commissure must also vary. He maintains that the
chiasma never reaches with its anterior border up to the limbus
sphenoidalis, but on an average is about 10 mm. from it. In
two adult subjects in which median sections of the head were
made after hardening in formol, I found the optic commissure
occupying practically a similar position to that figured in my
two plates.

[1] "The Position of the Optic Commissure," *Proceedings of the Anatomical
Society of Great Britain and Ireland*, May 1894.

[2] "Ueber die Lage und die Dimensionen des Chiasma opticum, u.s.w.,"
Vereinsbeilage d. deutsch. med. Wochensch., 1897.

The position of the optic commissure appears to vary according to the length of the optic nerves and the amount of cerebro-spinal fluid in the region of the interpeduncular space. It is often situated some little distance above the pituitary body, and may be found so far back as to lie vertically above the free upper edge of the dorsum sellæ. It thus appears that the situation of the optic commissure as shown in my Pl. I. and II. cannot be advanced as a proof of the displacement due to freezing.

In the whole literature of this subject only one figure of a frozen section of the head is known to Froriep which does not show undoubted artefacts due to freezing. This is a drawing by Axel Key and Retzius [1] of a median section of a head made after injecting the subarachnoid space and the ventricles. Froriep admits that certain parts of the brain are not quite normal, but he considers this to be due to the pressure of the material injected. In his opinion the most surprising thing in this case is that the pons and medulla occupy their natural position.

Enough has been already said to show that we do not agree with Froriep's contention that all the published plates of frozen sections through the unopened head (except the last mentioned) show distinct and undoubted signs of cerebral displacements. He is on firmer ground when he bases his opinion on the results of his own observations and experiments. These results in some cases are very surprising, but coming from an anatomist with such a high reputation as an accurate and a keen observer, they demand very careful consideration.

Froriep's attention appears to have been first directed to this question during the examination of a series of horizontal sections of the neck and thorax of a male subject aged 26 years. In these preparations the spinal cord was surrounded by an irregular whitish mass, which he found to consist of white and grey brain substance filling the dura mater sheath down to the level of the 5th dorsal vertebra. In another subject, a male 21 years old, the medulla and the spinal cord as far as the 4th cervical vertebra were surrounded on all sides by this material, and from this point to the 12th dorsal vertebra the spinal cord

[1] *Studien in der Anatomie des Nervensystems und des Bindegewebes*, erste Hälfte, Stockholm, 1875, Tafel vii. fig. 1.

was pressed towards the dorsal side of the spinal canal, while on its ventral side this brain material varied in thickness from 4 to 8 mm. In a frozen head which had been separated from the body, the spinal cord had bulged beyond the plane of the section through the neck. As in this case the vessels were filled with a turpentine and linseed oil paint injection, which process may have injured the parts, a fresh uninjected subject was selected and the head frozen after cutting through the neck between the 4th and 5th cervical vertebræ. At first the cut surface of the spinal cord was in the same plane as the divided vertebral column. After being in the freezing mixture for seventeen hours the spinal cord projected 3 mm. from the spinal canal, and five hours later a cylindrical mass 10 cm. long protruded beyond the vertebral canal. On median section the specimen presented appearances indicating that the lower parts of the brain had been pressed down and portions of it damaged. The pons was flattened against the base of the skull so as to reach down to the foramen magnum, and the hinder part of the thalamus and the mid-brain were depressed, while the inferior vermiform process, as well as the lower part of the lateral lobes of the cerebellum, had been displaced downwards in a much injured condition through the foramen magnum into the vertebral canal. In order to see if this expansion and consequent injury and displacement of the brain could be avoided by hardening the brain before freezing by injecting a fixing fluid, Froriep injected a 10 p.c. solution of formol into the vessels of a very fresh subject, and the freezing was not commenced until the tissues were well fixed by the formol. When the specimen was removed from the freezing mixture and examined, it was found that the spinal cord had not protruded beyond the cut surface of the neck, and it looked as though the previous fixation with formol had prevented the expansion of the brain during the freezing process. When, however, a median section of the frozen head was made, it was discovered that part of the base of the skull above the nasal cavities had been fractured and depressed, and a portion of the right frontal lobe of the brain pressed into the upper part of the nose, the ethmoidal cells, and even the frontal sinus.

In Froriep's experience the axial portions of the mid- and

hind-brain usually suffer more severely from the freezing than any other parts of the brain, and he explains this on the supposition that they are the last parts of the cranial contents to freeze, and are consequently compressed and displaced by the expansion of the more superficial portions of the brain, which freeze sooner. In the case of the formol-hardened brain, Froriep supposes that the neck was frozen earlier than usual and thus filled the upper part of the vertebral canal with a firm resisting mass.   Under these conditions the expanding brain had broken the weak anterior part of the base of the skull and forced the adjacent portion of the brain out of the cranial cavity.

While readily admitting the interest and importance of Froriep's results, I felt that they were so opposed not merely to my own experience, but also to the published results of other workers, as to require further observations before being accepted as of normal and regular occurrence.   Nearly all my frozen sections were made previous to the publication of my work on *The Topographical Anatomy of the Child*, which appeared in 1887, and with but few exceptions the brains of these specimens have not been preserved until the present time.   More recently, however, I have prepared and studied carefully a series of frozen sections of the head of a female, which was hardened in formol before freezing, and since then has been carefully preserved in that fluid.   The specimens and photographs of the sections were shown to the members of the Anatomical and Physiological Section of the Royal Academy of Medicine in Ireland, in Feb. 1896 (see *Proceedings* of this Academy, vol. xvi. p. 407). After reading Froriep's paper I decided to carefully examine these preparations to see whether or not the section showed those artefacts which were to be expected from Froriep's observations.   The head has been divided by horizontal cuts into six slabs, and so far as the surfaces of these slabs were concerned, I could find no indication of such displacement or injury, either to the brain or the skull.   As, however, Froriep refers frequently to the appearances of median sections of the lower parts of the brain, I cut in this plane three of the slabs (Nos 3, 4, and 5) which contained the mid-brain, pons cerebellum and medulla, and took a photograph (see Pl. XI.) of the left halves of these slabs after placing them in their proper relation

to one another. All the sections of this head, as well as photographs of both the horizontal and sagittal sections, were exhibited at a meeting of the Anatomical Society of Great Britain and Ireland in June 1902.

On comparing the divided parts of the brain seen in Pl. XI. with similar sections made on brains hardened and cut *in situ* without freezing, I could discover no essential differences in position or general appearance. In my view it is more normal than the plate in Axel Key and Retzius [1] which Froriep regards as free from any artefact due to the freezing. In their section the direction of the posterior part of the corpus callosum is quite different from that usually seen. They show the splenium directed nearly straight back, whereas it is almost invariably turned more or less directly downwards. Again, the lower end of the pons reaches within a $\frac{1}{4}$ of an inch of the anterior edge of the foramen magnum. It is true that in my specimen the lateral lobes of the cerebellum reached into the foramen magnum, but that is frequently seen in unfrozen heads, and cannot be regarded as a proof of the cerebellum having been forced down by the pressure of the brain tissue above expanding as it froze.

The method I adopted in the preparation of my specimen was as follows :—The entire body was hardened by the injection of a strong solution of formol, the neck divided opposite the 5th cervical vertebra, and the head again injected, but this time through the carotids and with a solution of gum ; the head was put into a wooden box just large enough to hold it, the box was filled with gum solution, and the closed box kept in a freezing mixture until well frozen. The box was then fixed in a frame and sawn across along with its contents.

I am not prepared to explain why Froriep's results differ from my own, but I am satisfied that the brain in my specimen did not suffer any appreciable displacement or injury as the result of the freezing process to which it was subjected, and I think this opinion is supported by the photograph on Pl. XI. which was made from my untouched life-size negative.

[1] *Op. cit.*

[*Life-size Photograph*

ON THE DEVELOPMENT OF THE PTERYGO-QUAD-RATE ARCH IN THE LACERTILIA. By R. Broom, M.D., B.Sc., C.M.Z.S.

THE development of the pterygo-quadrate arch in Sphenodon has recently been carefully worked out by Howes and Swinnerton (1), who have shown that in this primitive reptile the arch in its early condition is present as an irregular cartilage, shaped somewhat like a broad capital H. Of this the anterior part represents the epipterygoid and the pterygoid process, while the posterior portion and most of the cross bar represent the quadrate.

In the lizard, while the epipterygoid closely resembles that in Sphenodon, the quadrate differs in having, at least in the later stages of development, no connection with the epipterygoid, and not even a trace of an anterior process. Parker (2) failed, in working out the development of Lacerta, to find any connection between the quadrate and the epipterygoid, even in the early stages; and Gaupp (3), who appears to have been the only later worker at the subject, has also failed to demonstrate any cartilaginous connection between the two elements.

Believing that the lizards are the immediate descendants of forms moderately closely related to Sphenodon, I thought it probable that a connection between the epipterygoid and the quadrate would be found in the embryos of at least some lizards, even though it might be lost in Lacerta. I therefore made an examination of embryos of as many different Lacertilian types as I have at present at hand. These include members of the Agamidæ, Zonuridæ, Lacertidæ, Scincidæ, and Chamæleontidæ. Of each of the types, I have examined embryos of a stage corresponding to stage Q of Howes' and Swinnerton's Sphenodon paper. This stage represents that in which membrane bones have commenced to ossify, and in which most cartilaginous structures are for the first time fully chondrified. It is also the stage in which ancestral structures which may completely degenerate in later ontogeny, are most likely to be found in a

well developed condition. In all the types which I have
examined I have found evidences of a connection between the
quadrate and epipterygoid, and in three of them the connection
is present as a well chondrified bar.

Zonuridœ (type, *Zonurus polyzonus*, Smith, fig. 2).—In the
embryo Zonurus the condition of the pyterygo-quadrate arch at
stage Q bears a marked resemblance to that of Sphenodon (fig. 1).
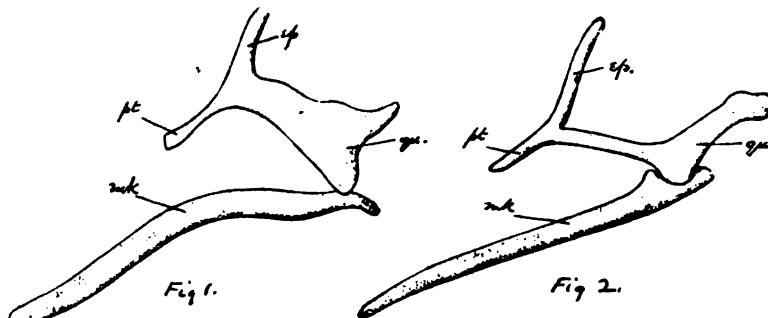
FIG. 1.—The mandibular and pterygo-quadrate cartilages of an embryo (stage Q)
     of *Sphenodon punctatus*, Grey (after Howes and Swinnerton).   × 14.
FIG. 2.—Ditto of embryo (stage Q) of *Zonurus polyzonus*, Smith.   × 24.

The epipterygoid, *ep.*, is present as a rounded, moderately
straight cartilaginous rod; at its lower end it curves forwards,
and is continued into a well developed cartilaginous pterygoid
process, *pt*, which rests on the pterygoid bone, and is more than
half the length of the epipterygoid. From the base of the
epipterygoid there runs backwards and slightly downwards to
near the lower end of the quadrate a rounded cartilaginous bar
of about the same thickness as the epipterygoid. The posterior
end of this connecting bar is slightly dilated, and is fixed to the
quadrate, *qu*, on its inner side, a little above the articular end.
The quadrate itself is moderately long and slightly curved, and
is directed well backwards. It is moderately round in section,
but from the outer and upper side of the anterior half there
passes upwards a small flattened ridge. The articular surface
for the lower jaw looks almost as much inwards as downwards.

Lacertidœ (type, *Eremias capensis*, Smith, fig. 3).—In the
embryo Eremias at stage Q, the epipterygoid, *ep*, is long and
slender. It is directed upwards, backwards, and slightly out-

wards. At its lower end it is continued into a short pterygodi process, *pt*, which is considerably more slender than the epipterygoid. Between the base of the epipterygoid and the quadrate there lies a strong cartilaginous connecting bar. The anterior end of this bar is of about the thickness of the epipterygoid, but on passing backwards it steadily increases in strength, till on reaching the quadrate it is more than twice the thickness of the epipterygoid. The quadrate, *qu*, is bent considerably backwards, and moderately stout.

Scincidæ (type, *Mabuia sulcata*, Peters, fig. 4).—In the embryo Mabuia the epipterygoid, *ep*, is present as a straight, uniformly thick rod of considerable length. At its lower end
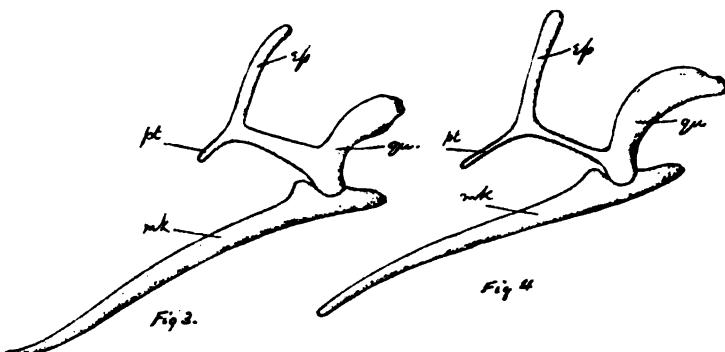
FIG. 3.—The mandibular and pterygo-quadrate cartilages of an embryo (stage Q) of *Eremias capensis*, Smith. × 40.

FIG. 4.—Ditto of embryo (stage Q) of *Mabuia sulcata*, Peters. × 32.

it is continued into a very slender cartilaginous pterygoid process, *pt*, which is more than half the length of the epipterygoid. The hinder part of the base of the epipterygoid is continued as a slender cartilaginous bar, which connects it with the quadrate. Both this connecting bar and the pterygoid process, though truly cartilaginous, show evidences of peripheral degeneration. The quadrate, *qu*, is well developed and gently curved backwards. It is much flattened, so that the concave surface looks more outwards than downwards or backwards. It receives the connecting bar just immediately above the articular surface.

Agamidæ (type, *Agama aculeata*, Merr., fig. 5).—It might

readily be expected that Agama, which is the lizard that appears to be most nearly related to Sphenodon, would show the quadrato-epipterygoid connection in a more developed condition than the more specialised lizards, but for some reason only a trace of the connection is found even in the embryo, and at no stage is it cartilaginous. At stage Q the epipterygoid, *ep*, is present as a very stout and relatively short cartilaginous rod, thicker above than below. From its base there passes backwards a very short cartilaginous spur towards the quadrate,
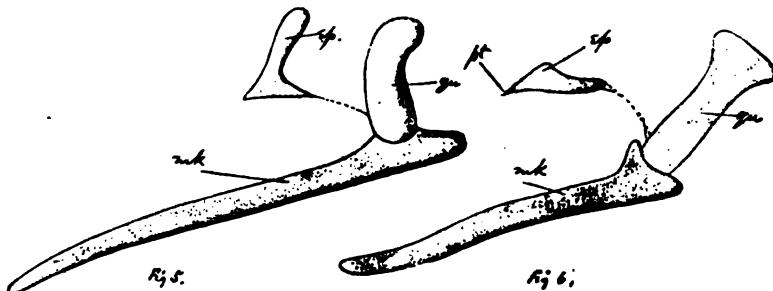
Fig. 5.—The mandibular and pterygo-quadrate cartilages of an embryo (stage Q) of *Agama aculeata*, Merr. × 23.

Fig. 6.—Ditto of an embryo (stage Q) of *Chamæleon melanocephalus*, Gray. × 33.

which is all that remains in a cartilaginous condition of the connecting bar. From the tip of the spur the line of the lost bar can be traced for some distance backwards distinctly as a cellular structure, which rests on the pterygoid bone, for a short distance indistinctly, and then on approaching the quadrate again distinctly as a cellular rod. There is only the merest vestige of a pterygoid process. At an earlier stage of development (stage P) the connecting bar is quite distinct, but it is not chondrified.

The quadrate, *qu*, is relatively stouter than in the other lizards examined, and is only very slightly inclined backwards.

Chamæleontidæ (type, *Chamæleon melanocephalus*, Gray, fig. 6).—The Chamæleon embryo differs from the other lizards in having only the vestige of an epipterygoid, *ep*. What may be regarded as the base of the epipterygoid, however, is distinct enough, and from it there pass forwards a short but distinct pterygoid process, *pt*, and, towards the quadrate, a cartilaginous

spur of moderate length, representing the connecting bar. From the tip of the spur a well marked series of cells, which are continued into the lower end of the quadrate, indicate the position occupied by the lost portion of the connecting rod. It will thus be seen that the condition of the inner portion of the pterygo-quadrate arch bears considerable resemblance to that of Agama.

The quadrate, *qu*, differs from that of the other forms in being straight, with an expanded upper end. It is considerably inclined backwards, and articulates with practically the end of the lower jaw, *mk*.

Conclusion.

The occurrence of a cartilaginous connection between the quadrate and epipterygoid in Lacertilian embryos of types so diverse as *Zonurus, Eremias* and *Mabuia* renders it practically certain that the immediate ancestors of the lizards were possessed of a fixed quadrate as in Sphenodon; and it thus becomes manifestly impossible to look upon the degree of fixity of the quadrate as a character of any great value in classification.

The change from the Sphenodon-like ancestral condition to that of the typical lizard was probably first started by the loss of the quadrato-jugal, which even in Sphenodon is somewhat rudimentary. When once the quadrate lost its attachment with the jugal, the posterior limb of the pterygoid would become more developed to compensate for the loss of the external arch; and with the increased development of the pterygoid the inner portion of the quadrate would readily become aborted and then lost, as the pterygoid would afford a better support than the epipterygoid.

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(3) Gaupp, E.

ON THE DEVELOPMENT AND HOMOLOGY OF THE MAMMALIAN CEREBELLAR FISSURES.[1] By O. CHARNOCK BRADLEY, M.B., *Professor of Anatomy, Royal Veterinary College, Edinburgh.* (PLATES XII–XVI.)

PART I.

VERY few serious attempts have been made to discover if there is any regular plan of arrangement of the fissures and lobes of the mammalian cerebellum. If we leave out of account those scattered descriptions of the cerebellum of a single animal, or of one or two animals—such, for instance, as Ganser's (1) classic and oft-quoted investigation into the anatomy of the brain of the mole, Krause's (2) monograph on the rabbit, and Miss Ärnbäck-Christie-Linde's (3) paper on the brain of the shrew and bat; not to mention more of a like nature—we find that the literature on the comparative anatomy of the cerebellum can only be described as meagre. Undoubtedly the best work that has been done in the way of attempting to clear away morphological difficulties is that which has appeared from the pen of Stroud (4). Another paper worthy of mention in this connection is that of Kuithan (5), which appeared almost contemporaneously with Stroud's. These two writers stand practically alone, inasmuch as they did not rest satisfied with an examination of the adult brain, but demanded to know what embryology had to say.. Stroud traced the development of the cerebellar fissures in the cat and in man; and Kuithan examined embryos of the sheep and man.

The latest attempt—as far as is known by the present writer—which has been made to establish the homology of the lobes of the cerebellum of mammals appears in the large work by Flatau and Jacobsohn (6) on the central nervous system. The value, great though it still remains, of this last piece of work is impaired by the fact that only adult material was used, and in many cases apparently second-hand descriptions were accepted.

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[1] The work, of which the present paper is the outcome, was done by the writer as a Research Student of the University of Edinburgh.

The ideal method, in a question of this kind, appears to be a combination of the embryological and the comparative anatomical. Stroud recognised this, and suggested that it would be necessary to examine into the intrauterine history of every mammal—a colossal task, verily. This being beyond the compass of the powers of one man, he examined two animals embryologically, and gave a long list of adult animals which he stated he had compared with each other. Unfortunately his description of the adult cerebella, seemingly promised in his first paper, is not as yet forthcoming.

Kuithan did not attempt the examination of a series of adult cerebella, but contented himself with the consideration of the development of the fissures in sheep and in man.

In the case of Stroud, Kuithan, and Flatau and Jacobsohn the investigation was apparently begun with the determination to find, if possible, homologies to the lobes of the cerebellum of man. To the mind of the present writer this was a mistake. In questions of this sort the brain of man should be lost sight of as far as possible, since it is admitted to be an organ which has far outdistanced, in its evolution, the brain of the average mammal. It is only after many (if possible, all) mammals have been passed under review that man may be brought in to complete the list as the highest and most richly endowed.

Acting upon the conviction that the brain of man should not be taken as the standard, but that the simplest cerebella should form the starting-point, the present investigation was commenced with a search for the smoothest and least complicated mammalian cerebellum. This was discovered—thanks in part to the paper of Miss Ärnbäck-Christie-Linde—in the shrew and some of the bats. The shrew's was therefore taken as the initial cerebellum; and had it been possible, shrew embryos would have been examined with a view to noting the time and order of appearance of the various fissures. Owing to the difficulty of obtaining a sufficiency of shrews at all periods of intrauterine life, and because of the comparative ease with which rabbit embryos of all ages could be obtained, it was decided to start the embryological part of the investigation with the latter; and indeed the rabbit possibly served the purpose better than the shrew would have done, since the

cerebellum of the adult is built on simple lines, and yet there
are parts in it in miniature which attain considerable magnitude
in the larger mammals.

Seeing that the rabbit has a cerebellum so very much more
simple than, say, that of the carnivora or the ungulates, it seemed
well that the development of the fissures in one of the larger
animals should also be watched. For this purpose, because of
the little difficulty in getting material, the pig was chosen. As
it happened, I was able to command material at practically
any stage of development, and therefore the ages of both the
rabbit and the pig embryos were, with one or two exceptions,
absolutely known.

In addition to the examination of the developmental history
of the fissures in two mammals, as many kinds of adult cerebella
as could be obtained have also been compared.

In this paper are stated the results of the investigation,
starting with an account of the appearance of the fissures in
the rabbit. Until the time arrives when it is necessary to
summarise results, the fissures and lobes will be known by
the simplest designations, viz., figures and letters, to the end
that the mind may not be influenced by the use of terms
which have acquired a certain fixed significance.

RABBIT.

20 *days embryo*, 37 *mm. long* (fig. 3).—When the entire
brain of the rabbit is examined at this stage, the cerebellum
appears as two fairly prominent lateral projections jutting out
on each side just below the mid-brain. A narrow connecting
band is also seen running transversely between the mid-brain
and the medulla. No fissures are visible to the naked eye;
and on making a sagittal microscopic section in the mesial
plane, the contour is even except at the posterior lower part
of the cerebellar lamina, where a curved hem-like portion is
marked off by a shallow fissure (fig. 3, IV.). This fissure makes
its first appearance about the 18th day (fig. 1). The hem-like
edge of the lamina is continued laterally over the lateral recess
of the ventricle, to become continuous with a similar lip belong-
ing to the medulla (fig. 2). It is apparently the Rautenlippe (His).

21 *days embryo*, 42 *mm. long* (fig. 4).—At this stage the cerebellum is very similar in appearance, to the naked eye, to that of the preceding day. The middle portion is somewhat more obvious, but no other visible change has occurred. A mesial sagittal section presents an outline which may be roughly described as triangular, the base of the triangle looking towards the medulla and pons. The two other sides of the triangle constitute what it will be convenient to call the anterior and posterior slopes of the cerebellum. Such a section again shows the fissure mentioned in the description of the 20 days embryo, but it is now farther removed from the extreme edge of the lamina (fig. 4, IV.). There is also a faint indication of another fissure at the upper part of the anterior slope (fig. 4, II.). It may be noted also that the future anterior medullary velum is better marked, as a result of a slight forward growth of the anterior part of the cerebellar lamina.

22 *days embryo*, 50 *mm. long* (figs. 5, 6 and 7).—A distinct advance has been made in development. The cerebellum is still very obviously made up of two prominent lateral masses, connected by a slighter intermediate portion, but the disparity in volume of these three parts is not so evident (fig. 5). In addition to a mere growth in size, other important changes have taken place. On an examination with the naked eye, it is clear that a portion of each lateral projection is about to be differentiated from the main bulk of the mass. This is shown by faint fissures, or rather grooves, slightly indenting the surface (figs. 5 and 6). Moreover, on sagittal section, the fissure, faintly foreshadowed in the 21 days embryo at the upper part of the anterior slope, is unmistakably a definite entity, and cuts the anterior slope into two almost equal parts (fig. 7, II.). The fissure which was the first to appear is still farther from the edge of the lamina (fig. 7, IV.). Further, there is the promise of a third fissure, this being indicated at this stage by a depression on the posterior slope (fig. 7, III.).

At this stage there are therefore evidences of three transverse fissures cutting at least the mesial part of the cerebellum into four portions; and in addition, indication of a subsequent complication of the lateral part.

23 *days embryo*, 50 *mm. long* (figs. 8, 9 and 10).—There is

now undoubted evidence of the rudiments of the three parts of the adult cerebellum. The central portion has increased considerably in volume, and there are shallow antero-posterior grooves marking off the future vermis and hemispheres.

The fissure on the posterior slope, which was not more than hinted at in the 22 days embryo, is now sufficiently deep to be visible by means of an ordinary pocket lens (fig. 8, III.). By the same means two transverse fissures are distinguishable on the anterior slope (fig. 9). The more superior corresponds to that already noticed in the previous stage. The lower one of the two is very shallow, and it is necessary to examine sections in order to be definitely certain that it is in reality the rudiment of a fissure.

Sagittal sections show three fissures, with the commencement of a fourth. The deepest corresponds to the one on the anterior slope of the 22 days cerebellum (fig. 10, II.).

In an embryo of 55 mm. in length, apparently some hours older than the one now under consideration, four fissures can be distinguished without any difficulty (fig. 11). It is desired to call especial attention to this stage, for it is believed that here we have the same number of fissures and lobes in the vermis as belong to the simplest form of mammalian cerebellum. Without applying any special names to these fissures and lobes, and without anticipating the attempt, which will be made later, to homologise them with similar features in the cerebella of other mammals, let it suffice for the present to designate the fissures as I., II., III. and IV., and the lobes as A, B, C, D and E, in each case commencing the enumeration anteriorly. Of the four fissures we may consider II. to stand in the first place of morphologic importance. It appears at an early date in all animals of which we have any embryo-logical account. Moreover, it maintains its supremacy of depth throughout the whole of embryonic life, and on into the adult state. As has been pointed out by previous writers, it is the deepest and most constant fissure of the cerebellum.

In the hemisphere of the 23 days embryo a fissure is growing inwards towards fissure III. of the vermis, and is consequently dividing the most lateral part of the hemisphere into two some-

what unequal parts, the more posterior of which projects the more laterally.

24 *days embryo*, 59 *mm. long* (fig. 12).—To the naked eye the only change is one of increased size and greater distinctness of the fissures. In microscopic sections the fissures are obviously deeper than they were in the preceding stage, and there are indications of a future fissure in lobe A (fig. 12, *c*).

25 *days embryo*, 64 *mm. long* (figs. 13, 14 and 15).—The distinction of vermis and hemispheres is now very clear, and the fissures are more definite. Fissure I. is now of considerable depth and extends completely across the vermis. Fissures II. and III. have invaded the groove marking vermis from hemisphere. The fissures indenting the lateral part of the hemispheres are deeper and approach fissure III. a little more closely. Two pairs of additional fissures can be distinguished in lobe C, these being in the groove between vermis and hemisphere; one pair on the anterior slope, the other on the posterior (fig. 13, *a*, fig. 14, *b*).

In sections, the fissure whose beginning was seen in lobe A of the 24 days cerebellum has attained some depth, and another fissure is forming below it. The former may be called, for the present, fissure *c* (fig. 15).

27 *days embryo*, 67 *mm. long* (figs. 16, 17 and 18).—All the fissures are deeper and much more lateral in extent. The outstanding projection of the hemisphere is now very sharply marked off from the rest of the hemisphere, and when the cerebellum is viewed from the front, is becoming separated from a smaller eminence which has developed in connection with the roof of the lateral recess of the ventricle. The upper and larger projection we shall henceforth speak of as the *paraflocculus*, and the lower as the *flocculus* (fig. 17). These terms were suggested by Stroud, and are useful as indicating that the two structures are not equivalent to the flocculus of man. They arise each in its own particular way. The paraflocculus is a part of the hemisphere proper. The flocculus, on the other hand, has developed in the same manner as lobe E, *i.e.* in close relationship to the Rautenlippe.

The two lateral fissures on the posterior slope of lobe C have now run together in the middle line, and constitute a single

transverse fissure cutting the lobe into two parts (fig. 16, *a*, fig. 18, *a*).

28 *days* (?) *embryo*, 67 *mm. long* (figs. 19, 20 and 21).—On the posterior slope the only change is one of depth and distinctness of the fissures, there being no additions. But when the cerebellum is viewed from the front, it is evident that development has here gone on more rapidly. Fissure II. is now in the form of a crescent, extending almost to the borders of the hemisphere. The fissures in the lateral parts of lobe C are also longer and deeper than in the stage described above. An additional fissure has made its appearance in lobe B. The paraflocculus and flocculus are separated by a still deeper depression, and the paraflocculus is more sharply separated from the rest of the hemisphere (fig. 20).

For the sake of subsequent description, we may indicate the fissure on the posterior slope which divides lobe C into two parts by the letter *a* (fig. 19, *a*, fig. 21, *a*). That this fissure, shallow though it is even in the adult rabbit, is of considerable morphologic importance, is brought out in the section of this paper which deals with the various adult cerebella.

At birth.—At the time when the rabbit is born, the cerebellum is not a replica in miniature of the adult organ, since development progresses rapidly for some days after birth.

The cerebellum at birth has its principal fissures of considerable depth, and some of its accessory fissures have begun to form (figs. 22 and 23). The paraflocculus is now completely surrounded by a fissure, with the exception of its posterior part, where there is no fissure, but merely a shallow depression. The flocculus is also completely bounded by a fissure, but as yet its surface is not sculptured by any lines. Fissure III. fades away in the groove or depression behind the paraflocculus, as also does fissure *a* (fig. 22). Even in the adult the lateral parts of these fissures are not deep.

2 *days after birth.*—After birth, as has been said, there is a fairly rapid change for a few days, until the cerebellum comes to resemble the adult organ.

At the end of the second day the exact connection of the paraflocculus with the vermis is more precisely indicated. Fissure III. has grown more laterally, and it is now evident

that the paraflocculus really belongs to lobe D. Lobe E can hardly be said to extend into the hemisphere at all, fissure IV. disappearing in the groove between vermis and hemisphere. In the earlier stages this lobe was continuous, without any fissure of demarcation with the posterior medullary velum; but from the 22nd day onwards it projects backwards more and more, and consequently a limiting fissure is formed.

Adult cerebellum (figs. 24, 25, 26 and 28).—In giving a description of the adult cerebellum of any animal, it is both convenient and rational to take fissure II. as the dividing line between an interior and a posterior portion. In the cerebellum of the rabbit this fissure lies wholly in the anterior surface, a surface presenting a concavity into which the mid-brain fits. Fissure II. occupies a comparatively high position in the vermis, but slopes rapidly downwards and outwards across the hemisphere to its border. Its great depth is brought out best by making a sagittal section of the vermis (fig. 28, II.). Below this fissure lie some seven folia, the two uppermost of which are separated from the rest by a fairly deep fissure, which we have seen makes its appearance about the 23rd day of intrauterine life, and which has been referred to in the previous paragraphs as fissure I. This is the deepest fissure in that part of the vermis which lies anterior to fissure II. When traced outwards it is found to fail to reach the extreme lateral border of the hemisphere (fig. 24, I.). At a distance of two folia below fissure I. is fissure c (as referred to in the embryonic cerebella), not quite so deep as the former, but reaching the lateral border. From the presence of fissure c lobe A is divided into two portions, which may be called lobule A_1 below the fissure, and lobule A_2 above it. In lobule A_1 the folia do not extend farther in a lateral direction than to a line corresponding to the lateral limits of the vermis, *i.e.* no hemisphere can be distinguished in this part of the cerebellum. The question of whether there is a lingula in the rabbit corresponding exactly to that of man is one which seems best answered in the negative. There are certainly no folia adherent to the anterior medullary velum.

The vermis and hemispheres behind fissure II. are divided into three lobes (C, D and E), corresponding to those first in-

ON THE DEVELOPMENT AND HOMOLOGY OF THE MAMMALIAN CEREBELLAR FISSURES.[1] By O. CHARNOCK BRADLEY, M.B., *Professor of Anatomy, Royal Veterinary College, Edinburgh.* (PLATES XII–XVI.)

PART I.

VERY few serious attempts have been made to discover if there is any regular plan of arrangement of the fissures and lobes of the mammalian cerebellum. If we leave out of account those scattered descriptions of the cerebellum of a single animal, or of one or two animals—such, for instance, as Ganser's (1) classic and oft-quoted investigation into the anatomy of the brain of the mole, Krause's (2) monograph on the rabbit, and Miss Árnbäck-Christie-Linde's (3) paper on the brain of the shrew and bat; not to mention more of a like nature—we find that the literature on the comparative anatomy of the cerebellum can only be described as meagre. Undoubtedly the best work that has been done in the way of attempting to clear away morphological difficulties is that which has appeared from the pen of Stroud (4). Another paper worthy of mention in this connection is that of Kuithan (5), which appeared almost contemporaneously with Stroud's. These two writers stand practically alone, inasmuch as they did not rest satisfied with an examination of the adult brain, but demanded to know what embryology had to say.. Stroud traced the development of the cerebellar fissures in the cat and in man; and Kuithan examined embryos of the sheep and man.

The latest attempt—as far as is known by the present writer —which has been made to establish the homology of the lobes of the cerebellum of mammals appears in the large work by Flatau and Jacobsohn (6) on the central nervous system. The value, great though it still remains, of this last piece of work is impaired by the fact that only adult material was used, and in many cases apparently second-hand descriptions were accepted.

[1] The work, of which the present paper is the outcome, was done by the writer as a Research Student of the University of Edinburgh.

The ideal method, in a question of this kind, appears to be a combination of the embryological and the comparative anatomical. Stroud recognised this, and suggested that it would be necessary to examine into the intrauterine history of every mammal—a colossal task, verily. This being beyond the compass of the powers of one man, he examined two animals embryologically, and gave a long list of adult animals which he stated he had compared with each other. Unfortunately his description of the adult cerebella, seemingly promised in his first paper, is not as yet forthcoming.

Kuithan did not attempt the examination of a series of adult cerebella, but contented himself with the consideration of the development of the fissures in sheep and in man.

In the case of Stroud, Kuithan, and Flatau and Jacobsohn the investigation was apparently begun with the determination to find, if possible, homologies to the lobes of the cerebellum of man. To the mind of the present writer this was a mistake. In questions of this sort the brain of man should be lost sight of as far as possible, since it is admitted to be an organ which has far outdistanced, in its evolution, the brain of the average mammal. It is only after many (if possible, all) mammals have been passed under review that man may be brought in to complete the list as the highest and most richly endowed.

Acting upon the conviction that the brain of man should not be taken as the standard, but that the simplest cerebella should form the starting-point, the present investigation was commenced with a search for the smoothest and least complicated mammalian cerebellum. This was discovered—thanks in part to the paper of Miss Ärnbäck-Christie-Linde—in the shrew and some of the bats. The shrew's was therefore taken as the initial cerebellum; and had it been possible, shrew embryos would have been examined with a view to noting the time and order of appearance of the various fissures. Owing to the difficulty of obtaining a sufficiency of shrews at all periods of intrauterine life, and because of the comparative ease with which rabbit embryos of all ages could be obtained, it was decided to start the embryological part of the investigation with the latter; and indeed the rabbit possibly served the purpose better than the shrew would have done, since the

cerebellum of the adult is built on simple lines, and yet there are parts in it in miniature which attain considerable magnitude in the larger mammals.

Seeing that the rabbit has a cerebellum so very much more simple than, say, that of the carnivora or the ungulates, it seemed well that the development of the fissures in one of the larger animals should also be watched. For this purpose, because of the little difficulty in getting material, the pig was chosen. As it happened, I was able to command material at practically any stage of development, and therefore the ages of both the rabbit and the pig embryos were, with one or two exceptions, absolutely known.

In addition to the examination of the developmental history of the fissures in two mammals, as many kinds of adult cerebella as could be obtained have also been compared.

In this paper are stated the results of the investigation, starting with an account of the appearance of the fissures in the rabbit. Until the time arrives when it is necessary to summarise results, the fissures and lobes will be known by the simplest designations, viz., figures and letters, to the end that the mind may not be influenced by the use of terms which have acquired a certain fixed significance.

RABBIT.

20 *days embryo*, 37 *mm. long* (fig. 3).—When the entire brain of the rabbit is examined at this stage, the cerebellum appears as two fairly prominent lateral projections jutting out on each side just below the mid-brain. A narrow connecting band is also seen running transversely between the mid-brain and the medulla. No fissures are visible to the naked eye; and on making a sagittal microscopic section in the mesial plane, the contour is even except at the posterior lower part of the cerebellar lamina, where a curved hem-like portion is marked off by a shallow fissure (fig. 3, IV.). This fissure makes its first appearance about the 18th day (fig. 1). The hem-like edge of the lamina is continued laterally over the lateral recess of the ventricle, to become continuous with a similar lip belonging to the medulla (fig. 2). It is apparently the Rautenlippe (His).

21 *days embryo*, 42 *mm. long* (fig. 4).—At this stage the cerebellum is very similar in appearance, to the naked eye, to that of the preceding day. The middle portion is somewhat more obvious, but no other visible change has occurred. A mesial sagittal section presents an outline which may be roughly described as triangular, the base of the triangle looking towards the medulla and pons. The two other sides of the triangle constitute what it will be convenient to call the anterior and posterior slopes of the cerebellum. Such a section again shows the fissure mentioned in the description of the 20 days embryo, but it is now farther removed from the extreme edge of the lamina (fig. 4, IV.). There is also a faint indication of another fissure at the upper part of the anterior slope (fig. 4, II.). It may be noted also that the future anterior medullary velum is better marked, as a result of a slight forward growth of the anterior part of the cerebellar lamina.

22 *days embryo*, 50 *mm. long* (figs. 5, 6 and 7).—A distinct advance has been made in development. The cerebellum is still very obviously made up of two prominent lateral masses, connected by a slighter intermediate portion, but the disparity in volume of these three parts is not so evident (fig. 5). In addition to a mere growth in size, other important changes have taken place. On an examination with the naked eye, it is clear that a portion of each lateral projection is about to be differentiated from the main bulk of the mass. This is shown by faint fissures, or rather grooves, slightly indenting the surface (figs. 5 and 6). Moreover, on sagittal section, the fissure, faintly foreshadowed in the 21 days embryo at the upper part of the anterior slope, is unmistakably a definite entity, and cuts the anterior slope into two almost equal parts (fig. 7, II.). The fissure which was the first to appear is still farther from the edge of the lamina (fig. 7, IV.). Further, there is the promise of a third fissure, this being indicated at this stage by a depression on the posterior slope (fig. 7, III.).

At this stage there are therefore evidences of three transverse fissures cutting at least the mesial part of the cerebellum into four portions; and in addition, indication of a subsequent complication of the lateral part.

23 *days embryo*, 50 *mm. long* (figs. 8, 9 and 10).—There is

now undoubted evidence of the rudiments of the three parts of the adult cerebellum. The central portion has increased considerably in volume, and there are shallow antero-posterior grooves marking off the future vermis and hemispheres.

The fissure on the posterior slope, which was not more than hinted at in the 22 days embryo, is now sufficiently deep to be visible by means of an ordinary pocket lens (fig. 8, III.). By the same means two transverse fissures are distinguishable on the anterior slope (fig. 9). The more superior corresponds to that already noticed in the previous stage. The lower one of the two is very shallow, and it is necessary to examine sections in order to be definitely certain that it is in reality the rudiment of a fissure.

Sagittal sections show three fissures, with the commencement of a fourth. The deepest corresponds to the one on the anterior slope of the 22 days cerebellum (fig. 10, II.).

In an embryo of 55 mm. in length, apparently some hours older than the one now under consideration, four fissures can be distinguished without any difficulty (fig. 11). It is desired to call especial attention to this stage, for it is believed that here we have the same number of fissures and lobes in the vermis as belong to the simplest form of mammalian cerebellum. Without applying any special names to these fissures and lobes, and without anticipating the attempt, which will be made later, to homologise them with similar features in the cerebella of other mammals, let it suffice for the present to designate the fissures as I., II., III. and IV., and the lobes as A, B, C, D and E, in each case commencing the enumeration anteriorly. Of the four fissures we may consider II. to stand in the first place of morphologic importance. It appears at an early date in all animals of which we have any embryological account. Moreover, it maintains its supremacy of depth throughout the whole of embryonic life, and on into the adult state. As has been pointed out by previous writers, it is the deepest and most constant fissure of the cerebellum.

In the hemisphere of the 23 days embryo a fissure is growing inwards towards fissure III. of the vermis, and is consequently dividing the most lateral part of the hemisphere into two some-

what unequal parts, the more posterior of which projects the more laterally.

24 *days embryo*, 59 *mm. long* (fig. 12).—To the naked eye the only change is one of increased size and greater distinctness of the fissures. In microscopic sections the fissures are obviously deeper than they were in the preceding stage, and there are indications of a future fissure in lobe A (fig. 12, *c*).

25 *days embryo*, 64 *mm. long* (figs. 13, 14 and 15).—The distinction of vermis and hemispheres is now very clear, and the fissures are more definite. Fissure I. is now of considerable depth and extends completely across the vermis. Fissures II. and III. have invaded the groove marking vermis from hemisphere. The fissures indenting the lateral part of the hemispheres are deeper and approach fissure III. a little more closely. Two pairs of additional fissures can be distinguished in lobe C, these being in the groove between vermis and hemisphere; one pair on the anterior slope, the other on the posterior (fig. 13, *a*, fig. 14, *b*).

In sections, the fissure whose beginning was seen in lobe A of the 24 days cerebellum has attained some depth, and another fissure is forming below it. The former may be called, for the present, fissure *c* (fig. 15).

27 *days embryo*, 67 *mm. long* (figs. 16, 17 and 18).—All the fissures are deeper and much more lateral in extent. The outstanding projection of the hemisphere is now very sharply marked off from the rest of the hemisphere, and when the cerebellum is viewed from the front, is becoming separated from a smaller eminence which has developed in connection with the roof of the lateral recess of the ventricle. The upper and larger projection we shall henceforth speak of as the *paraflocculus*, and the lower as the *flocculus* (fig. 17). These terms were suggested by Stroud, and are useful as indicating that the two structures are not equivalent to the flocculus of man. They arise each in its own particular way. The paraflocculus is a part of the hemisphere proper. The flocculus, on the other hand, has developed in the same manner as lobe E, *i.e.* in close relationship to the Rautenlippe.

The two lateral fissures on the posterior slope of lobe C have now run together in the middle line, and constitute a single

transverse fissure cutting the lobe into two parts (fig. 16, *a*, fig. 18, *a*).

28 *days* (?) *embryo*, 67 *mm. long* (figs. 19, 20 and 21).—On the posterior slope the only change is one of depth and distinctness of the fissures, there being no additions. But when the cerebellum is viewed from the front, it is evident that development has here gone on more rapidly. Fissure II. is now in the form of a crescent, extending almost to the borders of the hemisphere. The fissures in the lateral parts of lobe C are also longer and deeper than in the stage described above. An additional fissure has made its appearance in lobe B. The paraflocculus and flocculus are separated by a still deeper depression, and the paraflocculus is more sharply separated from the rest of the hemisphere (fig. 20).

For the sake of subsequent description, we may indicate the fissure on the posterior slope which divides lobe C into two parts by the letter *a* (fig. 19, *a*, fig. 21, *a*). That this fissure, shallow though it is even in the adult rabbit, is of considerable morphologic importance, is brought out in the section of this paper which deals with the various adult cerebella.

At birth.—At the time when the rabbit is born, the cerebellum is not a replica in miniature of the adult organ, since development progresses rapidly for some days after birth.

The cerebellum at birth has its principal fissures of considerable depth, and some of its accessory fissures have begun to form (figs. 22 and 23). The paraflocculus is now completely surrounded by a fissure, with the exception of its posterior part, where there is no fissure, but merely a shallow depression. The flocculus is also completely bounded by a fissure, but as yet its surface is not sculptured by any lines. Fissure III. fades away in the groove or depression behind the paraflocculus, as also does fissure *a* (fig. 22). Even in the adult the lateral parts of these fissures are not deep.

2 *days after birth.*—After birth, as has been said, there is a fairly rapid change for a few days, until the cerebellum comes to resemble the adult organ.

At the end of the second day the exact connection of the paraflocculus with the vermis is more precisely indicated. Fissure III. has grown more laterally, and it is now evident

that the paraflocculus really belongs to lobe D. Lobe E can hardly be said to extend into the hemisphere at all, fissure IV. disappearing in the groove between vermis and hemisphere. In the earlier stages this lobe was continuous, without any fissure of demarcation with the posterior medullary velum; but from the 22nd day onwards it projects backwards more and more, and consequently a limiting fissure is formed.

Adult cerebellum (figs. 24, 25, 26 and 28).—In giving a description of the adult cerebellum of any animal, it is both convenient and rational to take fissure II. as the dividing line between an interior and a posterior portion. In the cerebellum of the rabbit this fissure lies wholly in the anterior surface, a surface presenting a concavity into which the mid-brain fits. Fissure II. occupies a comparatively high position in the vermis, but slopes rapidly downwards and outwards across the hemisphere to its border. Its great depth is brought out best by making a sagittal section of the vermis (fig. 28, II.). Below this fissure lie some seven folia, the two uppermost of which are separated from the rest by a fairly deep fissure, which we have seen makes its appearance about the 23rd day of intrauterine life, and which has been referred to in the previous paragraphs as fissure I. This is the deepest fissure in that part of the vermis which lies anterior to fissure II. When traced outwards it is found to fail to reach the extreme lateral border of the hemisphere (fig. 24, I.). At a distance of two folia below fissure I. is fissure c (as referred to in the embryonic cerebella), not quite so deep as the former, but reaching the lateral border. From the presence of fissure c lobe A is divided into two portions, which may be called lobule A_1 below the fissure, and lobule A_2 above it. In lobule A_1 the folia do not extend farther in a lateral direction than to a line corresponding to the lateral limits of the vermis, *i.e.* no hemisphere can be distinguished in this part of the cerebellum. The question of whether there is a lingula in the rabbit corresponding exactly to that of man is one which seems best answered in the negative. There are certainly no folia adherent to the anterior medullary velum.

The vermis and hemispheres behind fissure II. are divided into three lobes (C, D and E), corresponding to those first in-

dicated in the 22 days embryo. Lobe C of the vermis usually
carries eight folia, the majority of which are not carried directly
into the hemisphere. The fissures between these folia are for
the most part shallow, but two of them go to a greater depth
than the rest, and are held to be of greater importance. Not only
are they deeper than the others, but they appear at an earlier
period. A reference to the 25 days embryo shows the fore-
runners of these fissures as two pairs of depressions; one on the
anterior, the other on the posterior slope. In the adult brain
the more anterior of the two occurs between folia 2 and 3
(counting from fissure II.), and on being traced into the hemi-
sphere is seen to run for some distance parallel to fissure II.,
into which it ultimately opens. For more immediate purposes
we shall speak of this fissure as fissure b (fig. 24, b, fig. 28, b).
An offshoot leaves it in the groove between vermis and hemi-
sphere, and curves outwards and backwards to the border of
the hemisphere.

The other deep fissure of lobe C separates folium 6 from
folium 7, and corresponds to the fissure resulting from the union
of the pair of grooves on the posterior slope which first appeared
on the 25th day, and which met in the vermis two days later.
This has already been referred to as fissure a. In the adult it
can be traced to the outermost limits of lobe C. If we recognise
the fissures just mentioned as being of importance, it follows
that lobe C must be looked upon as consisting of three portions
or lobules. These, for the present, will be called lobules C_1,
C_2 and C_3, starting the enumeration anteriorly.

The fissure between lobes C and D (fissure III.) is of moderate
depth in the middle of the vermis (fig. 28, III.), but becomes
very shallow at its lateral borders. In some specimens, how-
ever, there is not much difficulty in tracing its curved course
outwards and upwards until it is lost in the deep fissure which
separates the paraflocculus from the rest of the hemisphere.
Lobe D is confined to the vermis, but in most specimens there
is a low white ridge connecting it with the paraflocculus. Its
surface is formed by three folia (sometimes a shallow fissure
divides the lowest folium into two). Of the two fissures
between these folia the lower is slightly the deeper, and the
lower folium extends rather farther towards the hemisphere

than the other two. These facts are mentioned because of the belief that lobe D of the rabbit corresponds to two lobules in more complicated cerebella.

Lobe E is entirely confined to the inferior aspect of the cerebellum, and, like lobe D, has no direct continuation into the hemisphere.

The paraflocculus projects markedly from the lateral part of the hemisphere, from which it is separated by a deep fissure in front and above, and by a depression behind. It is entirely enclosed in a special fossa formed by the temporal bone (lobulus petrosus). As has been seen in tracing its development, it is really a piece of the hemisphere which has been cut off from the rest. Its developmental connection with lobe D is a point upon which it is desired to lay emphasis.

The flocculus consists of two or three folia, seen best when the cerebellum is viewed from the front, and lying anterior to the paraflocculus (fig. 25). It is in contact with the lateral extremity of lobe B, from which it is separated by a fissure which contains the middle cerebellar peduncle (fig. 24).

Lepus timidus (fig. 27).—The differences between the cerebellum of the rabbit and that of the hare are not perhaps very great, but they seem sufficiently important to merit mention. Lobes A, B and C are practically identical with those of the rabbit. Lobe C has again eight folia in the vermis, and a fissure, *a*, deeper than the rest, separates folia 6 and 7. This fissure is much more definite in hemisphere of the hare than it is in the rabbit.

The most important differences exist in lobe D. Here the number of folia is at least four, as against three in the rabbit; and the uppermost of the four is more definitely joined to the paraflocculus by a ridge which is slightly foliated along its upper border as it approaches the paraflocculus. This fact is mentioned as being the ground upon which the statement, that in the adult rabbit lobe D is connected with the paraflocculus, is based. In many specimens of the rabbit's cerebellum the adult connection is obscure; therefore the evidence afforded by the brain of the hare is welcome.

Before passing to the consideration of the development of the much more complicated cerebellum of the pig, it is perhaps

well to describe those adult cerebella which are built on the same or similar lines as obtain in the rabbit.

Sorex vulgaris (fig. 29).—As previously stated, apparently the simplest form of mammalian cerebellum is found in the shrew and some of the bats. An examination of sagittal sections of the shrew's cerebellum shows that the vermis is divided into fine lobes by four fissures, *i.e.* that the numerical condition as found in the brain of a rabbit embryo of about 24 days is maintained into adult life. · Fissure I. is of moderate depth, but does not extend much, if at all, beyond the vermis. Fissure II., on the other hand, is very deep, and passes far out into the hemisphere. Its importance as a morphologic entity probably stands out more plainly in the shrew, and some few animals with a similar simple cerebellum, than it does in many of those in which the fissures are more numerous.

Fissure III. is the shallowest of the fissures of the vermis, and does not invade the hemisphere, or at any rate only slightly. There is a fissure in the hemisphere occupying a corresponding position, but microscopic sections show that there is no union of the two. Fissure IV. very early disappears in a series of sections. There is a projection, from the lateral part of the hemisphere, enclosed in a cell in the temporal bone, and doubtless corresponding to the paraflocculus of the rabbit. It seems very doubtful if a flocculus proper is developed.

Erinaceus Europœus (figs. 30, 31, 32, 33 and 34).—The hedgehog has a cerebellum which, in degree of complexity, may be considered to stand between that of the shrew and that of the rabbit. The vermis is divided into five lobes by four fissures, of which the second (fissure II.) is by far the deepest. This is visible in the vermis when the cerebellum is examined from above, but it leaves the dorsal to gain the anterior surface in the shallow groove which marks vermis from hemisphere. In the hemisphere it slopes rapidly downwards and outwards, in much the same manner as in the rabbit. Fissure I. is second in point of depth. Unlike the corresponding fissure in the rabbit, it reaches the borders of the hemispheres. Fissures III. and IV. are of moderate depth, and run into one another at the lateral boundary of the vermis.

Lobe A is, as a rule, beset by three folia, and, unlike the

corresponding lobe in the rabbit, is not divided by a fissure, *c*. Lobe B has never more than two folia, so far as can be gathered from an examination of some ten brains.   Lobe C has five folia in the vermis, the four anterior of which are separated from the fifth by a fissure which corresponds to *a* in the brain of the rabbit, and which is continued into the hemisphere in a like manner.   Lobe C, anterior to fissure *a*, becomes much expanded in the hemisphere, and its folia are increased in number.   The folium behind fissure *a* retains its single character after its prolongation into the hemisphere (lobule C_3).   Lobes D and E have each two folia, and are confined to the vermis.

The paraflocculus is fairly well marked, but does not produce the projection (lobulus petrosus) which is so prominent in the rabbit.   The flocculus is rather smaller in the hedgehog than in the rabbit, but has approximately the same position and shape as in the latter animal.   Sagittal sections show very clearly the close relationship of this lobule with the posterior medullary velum.   As successive sections are examined in a direction away from the vermis, the velum is seen to become thickened by grey matter, which is directly continuous with the grey matter of the flocculus.

Talpa Europœa (figs. 35, 36 and 37).—In the vermis of the cerebellum of the mole, the four fundamental fissures are easily distinguished.   Fissure I. is relatively a slightly greater depth than in either the rabbit or the shrew.   It is, as usual, limited to the anterior surface, and runs almost vertically downwards in the line of boundary between vermis and hemisphere. Fissure II. is of very considerable depth.   Its course is very sinuous, beginning on the anterior surface of the vermis, then taking a sharp bend backwards over the anterior superior border of the cerebellum to gain the dorsal surface, where it again turns sharply forwards and outwards to once more become included in the anterior surface, down which it runs almost vertically.   Fissure III. is more distinct than in the shrew. Fissure IV. is of about the same depth as in Sorex.

Lobe A is almost entirely in the vermis, though it expands a little in the lower part of the anterior surface.   Its surface possesses two fissures, the lower of which is more pronounced,

and may possibly be comparable to fissure *c* of the rabbit; a fissure not represented in the shrew. Lobe B is constricted in the vermis, where it is constituted by a single folium; but, owing to the erratic course taken by fissure II., it expands considerably in the hemisphere. That part of lobe C which is included in the vermis is comparatively extensive. This lobe is constricted at the junction of vermis and hemisphere, to become again extensive in the hemisphere itself. There are a few shallow fissures in the vermis, but one of them is of slightly greater depth than the rest, and corresponds to fissure *a*. Lobule C_3 consists of a narrow folium in the vermis, but expands in the hemisphere (fig. 35). This is a point of some moment, because in the more complicated cerebella, to be hereafter described, the expansion of this particular lobule in the hemisphere is a prominent feature. Lobes D and E are simple and call for no remark, except that a very thin and narrow band runs outwards and forwards from D, but is entirely hidden by the bulk of the hemisphere. This band extends as far forwards as the base of the paraflocculus.

The paraflocculus is in the form of a rounded lobule, with fissured surface, connected with the hemisphere by a narrow neck, and enclosed in a fossa of the temporal bone. No flocculus can be made out with certainty.

Mus decumanus (figs. 38, 39, 40 and 41).—The cerebellum of the rat is decidedly more complicated than that organ in the mole or hedgehog, and approaches more nearly that of the rabbit. Fissures I. and II. resemble those of the rabbit, except that I. always reaches the margin of the hemisphere, and the central part of II. is visible of the dorsal surface. Fissures III. and IV. are also very similar to those of the rabbit's cerebellum.

Lobe A is divided into two parts by a fissure, *c*, which is almost as deep as I. The upper part of this lobe (lobule A_2) has two folia; the lower part (lobule A_1) a variable number, separated by shallow fissures (fig. 41). Lobe B has two folia, and resembles the like lobe in the rabbit both in position and size. In lobe C there is a deep fissure, *a*, cutting the vermis to almost the same depth as fissure III., and separating a single folium, which is continued into the hemisphere. The rest of lobe C, which is contained in the vermis, has about three folia,

of which the most anterior is the largest. A definite fissure, b, cannot be made out. The hemisphere part of lobe C, anterior to fissure a, is of considerable size. Lobes D and E are confined to the vermis, the former having three folia, the latter two.

The paraflocculus projects from the hemisphere by a narrow neck, and is received into a fossa in the temporal bone, the investment of bone being less close than in the rabbit. There is a small, simple flocculus lying anterior to the paraflocculus, and touching the lateral borders of lobes A and B.

In the mouse (*Mus musculus*) the cerebellum very closely resembles that of the rat. The paraflocculus has possibly a slightly narrower neck and is more closely invested by bone.

Arvicola amphibius (figs. 42, 43 and 44).—The water-vole has a cerebellum which differs from that of the brown rat in minor points only. Its fissures are the same in number. As a rule, fissure I. does not quite reach the border of the hemisphere. Lobe A is divided by a fairly deep fissure, c. Lobule A_2 has two folia, lobule A_1 only one. Lobe B is narrow (as in the rat), and possesses two folia in the vermis. The vermis portion of lobe C has six folia, fissure a separating the sixth from the rest. The sixth folium (constituting the central part of lobule C_3) is continued into the hemisphere without either increase in size or accession of fissures. There is possibly a fissure, b, placed between the 2nd and 3rd folia, and continued outwards and forwards into the anterior surface of the hemisphere.

Lobes D and E are limited to the vermis, D having two folia, E only one. The paraflocculus and flocculus are almost identical with those in the rat.

The cerebellum of the field-vole (*Arvicola agrestis*, fig. 45) only differs from that of the water-vole inasmuch as its folia are fewer in number.

Pteropus poliocephalus (figs. 46, 47, 48 and 49).—A sagittal section through the middle of the vermis of this large bat discloses an arrangement of lobes not very unlike that of the hedgehog. The number of lobes and fissures is the same, but the folia are somewhat more numerous. Fissure I. is rather shallow, but fissure II. is of great depth; of fissures III. and IV. there is nothing remarkable to note. Lobe A is small and carries about three folia. There is apparently no fissure c. Lobe B, on the

other hand, is large, and is provided with five or six folia. There are seven folia in the vermis in lobe C, the seventh of which is separated from those anterior to it by an unmistakable fissure *a*. This single folium of the vermis is connected with two folia in the hemisphere. In Talpa, lobule C_3 increased in size in the hemisphere, but did not acquire any intrinsic fissures. In Pteropus it also expands, and in addition is sculptured by a fissure. It seems good to call attention to this point, in the light of other facts presently to be set forth. Lobes D and E belong exclusively to the vermis; the former has three folia, the latter two.

A noteworthy development appears in the paraflocculus. It consists of two parts, an upper and a lower. In the cerebella to be described in the following pages, the morphologic import- ance of this feature of the paraflocculus will become evident. The lower portion of the paraflocculus of Pteropus consists of a lobulus petrosus; *i.e.* it projects into a bony fossa and has a narrow neck. Both portions of the paraflocculus are foliated (figs. 46 and 47). The flocculus is small, and divided into two by an almost vertical fissure, only seen when the cerebellum is viewed from the side.

It is interesting to notice the great difference in the cere- bellum of the Megachiroptera as shown in Pteropus, and that of the Microchiroptera as exemplified in *Vesperugo pipestrellus*, described and figured by Miss Ärnbäch-Christie- Linde (3). Vesperugo has a cerebellum not more complex than that of the shrew, whereas the cerebellum of Pteropus is as complex as that of the rabbit, or possibly more so.

Sciurus vulgaris (figs. 50, 51, 52 and 53).—The squirrel offers a most instructive degree of complexity in the fissures and lobes of its cerebellum, inasmuch as it exhibits a condition intermediate between the simpler forms, which have already been described, and those of a more complicated nature, still to be considered. For this reason the squirrel's cerebellum is peculiarly serviceable to anyone desiring to establish homologies in the lobes and fissures of mammals in general.

Fissure I. in the squirrel, as in the rabbit, stands second in point of depth. Also, as in the rabbit, it fails to reach the margin of the hemisphere. Fissure II. is far and away the

deepest of all the fissures. It is visible in the vermis, on the dorsal surface; but turning forwards abruptly, it runs down the anterior surface of the hemisphere, with only a slight degree of obliquity. Fissure III. is of considerable depth, and on reaching the border of the vermis, turns at almost a right angle, and runs nearly vertically downwards for some distance. Then, curving outwards and afterwards forwards, it is traceable into the deep fissure separating the paraflocculus from the hemisphere (figs. 51 and 52, III.). Fissure IV. resembles the same fissure in the rabbit, and offers no noteworthy feature.

The greatest interest centres itself in the lobes. Lobe A is of considerable size, consists of five folia, and is indented by a fissure, c, between the 2nd and 3rd folia. Another fissure, of a depth almost equal to that of c, occurs at a distance of two folia below the latter. Lobe B consists of three or four folia and is not very noteworthy. Lobe C has five folia in the vermis. The anterior four expand in the hemisphere, in the customary manner, and are separated from the fifth by a fissure, a. The fifth folium, instead of remaining as a single folium when traced into the hemisphere, as in the rabbit, suddenly expands and forms a not inconsiderable lobule, clearly differentiated from the rest of lobe C by a continuation of fissure a (fig. 52). Lobe D is relatively large and carries six folia. It is divided into two approximately equal parts by a fissure of a depth only slightly, if at all, inferior to that of fissure III. We shall refer to this latest fissure as d in future descriptions, as its value as a division between parts of the vermis is unquestionable (figs. 51, 52 and 53, d). That part of lobe D which lies above fissure d (and which we may call lobule D_1) consists of two folia, which becoming one, curves round the inferior border of lobule C_3, and losing its grey cortex, gives place to a white ridge passing directly to the upper part of the paraflocculus. That part of lobe D inferior to fissure d (known in the succeeding descriptions as lobule D_2) is not continued into the hemisphere. Lobe E is comparatively small, and consists of only one definite folium.

The paraflocculus is large when compared with the similar lobule of the cerebella already described, and presents the appearance of a rounded foliated band which has been doubled upon itself and placed with its long axis approximately in the

direction of the long axis of the head. The bend is in front (figs. 51 and 52). The flocculus is small and compressed. It lies below the paraflocculus, and can only be seen from the side or front of the cerebellum.

The points in the foregoing description to which it is desired to draw especial attention are as follows :—(1) The increasing complexity of lobe A as compared with the same lobe of all the other animals so far discussed. (2) The considerable expansion in the hemisphere of lobule C_3. (3) The division of lobe D into two parts by the fissure d, and the lateral continuation of the upper part (lobule D_1) of this lobe. (4) The arrangement of the paraflocculus in the form of two parallel portions, continuous with each other in front, and the connection of lobule D_1 with the upper portion of the paraflocculus.

The cerebella which remain to be described are all built on much more complicated lines than are those which have been passed under view in the foregoing sections. This being so the examination of the development of the fissures in an animal possessing a richly fissured and foliated cerebellum in adult life will greatly aid in the task of recognising homologies. Therefore pig embryos will be examined, with a view to noting the time and order of appearance of the various fissures.

(To be continued.)

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[PLATE XII.
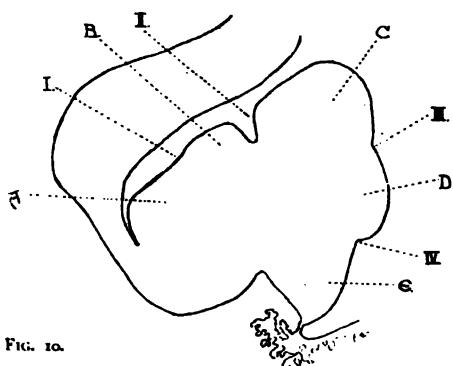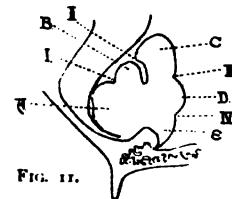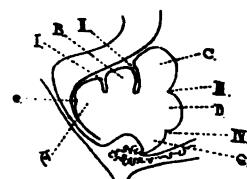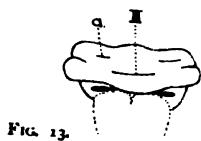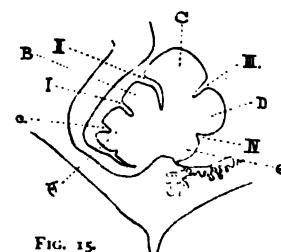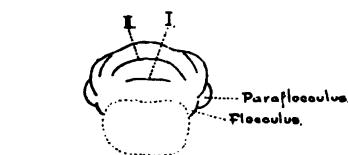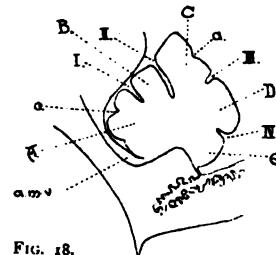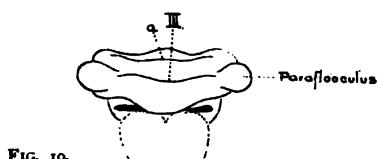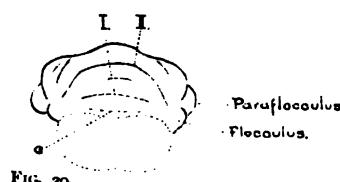
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FIG. 21.

FIG. 22.

Paraflocculus.

Paraflocculus
Flocculus

FIG. 23.

Paraflocculus.
Flocculus.

Paraflocculus

Flocculus

FIG. 24.

Flocculus.

FIG. 25.

Paraflocculus

Paraflocculus

FIG. 26.

Paraflocculus
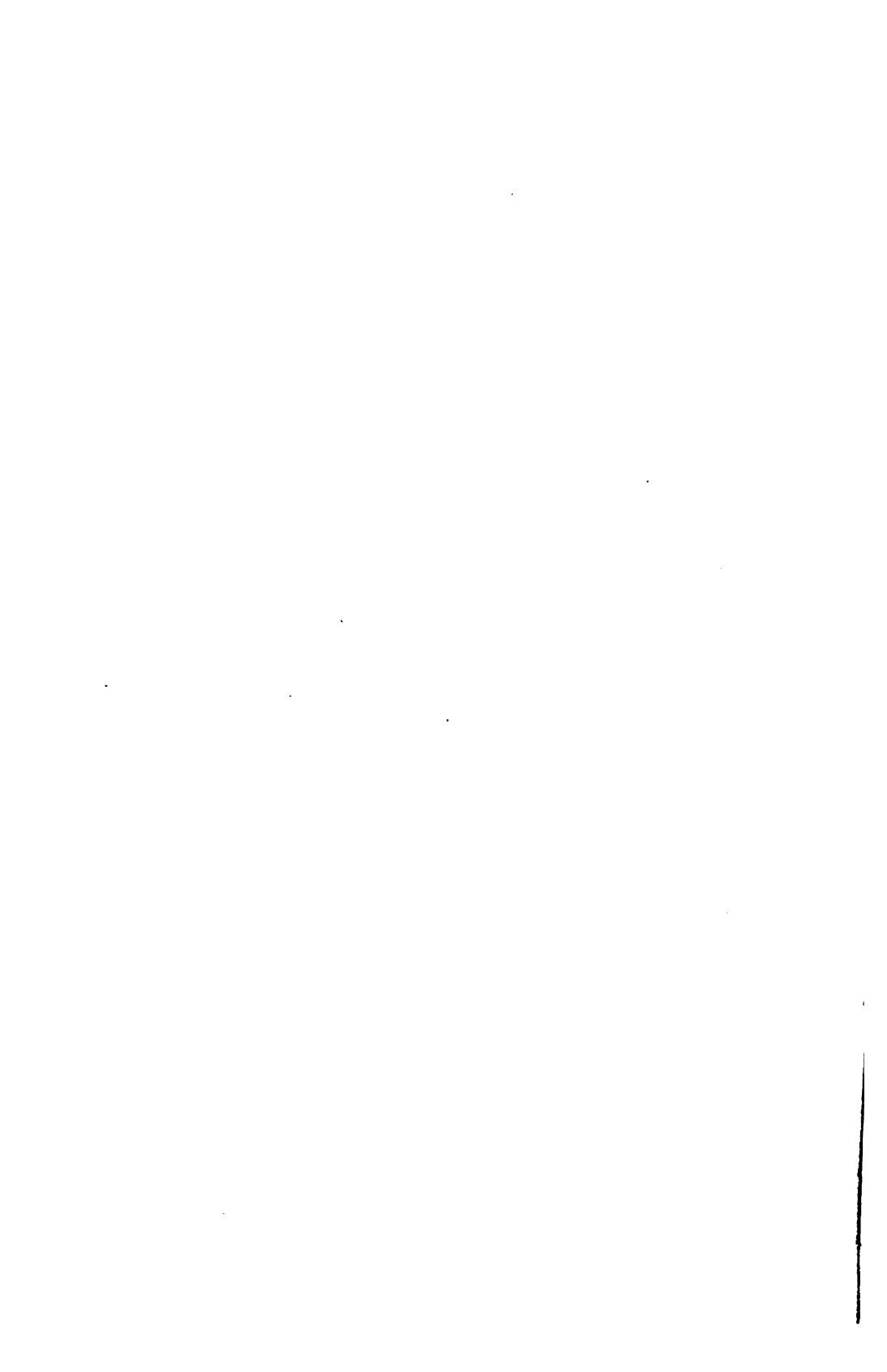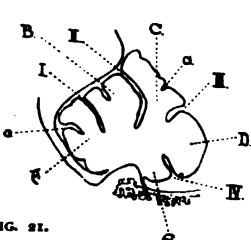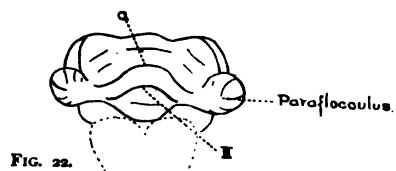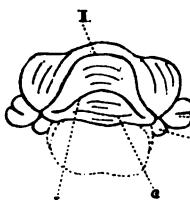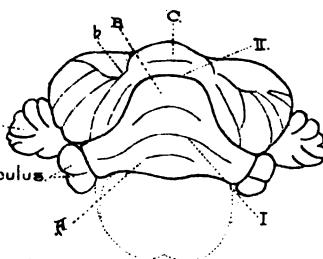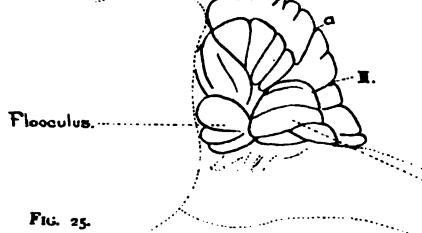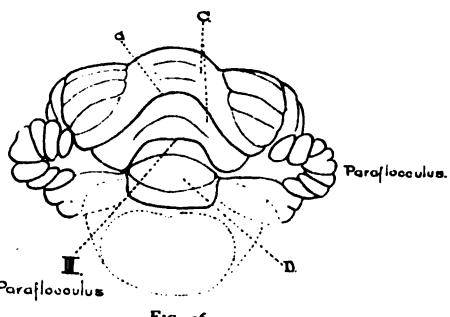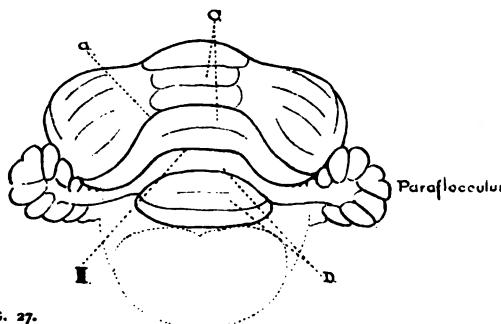
FIG. 27.

FIG. 28.

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Homology of the Mammalian Cerebellar Fissures.

[PLATE XV.

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Homology of the Mammalian Cerebellar Fissures.
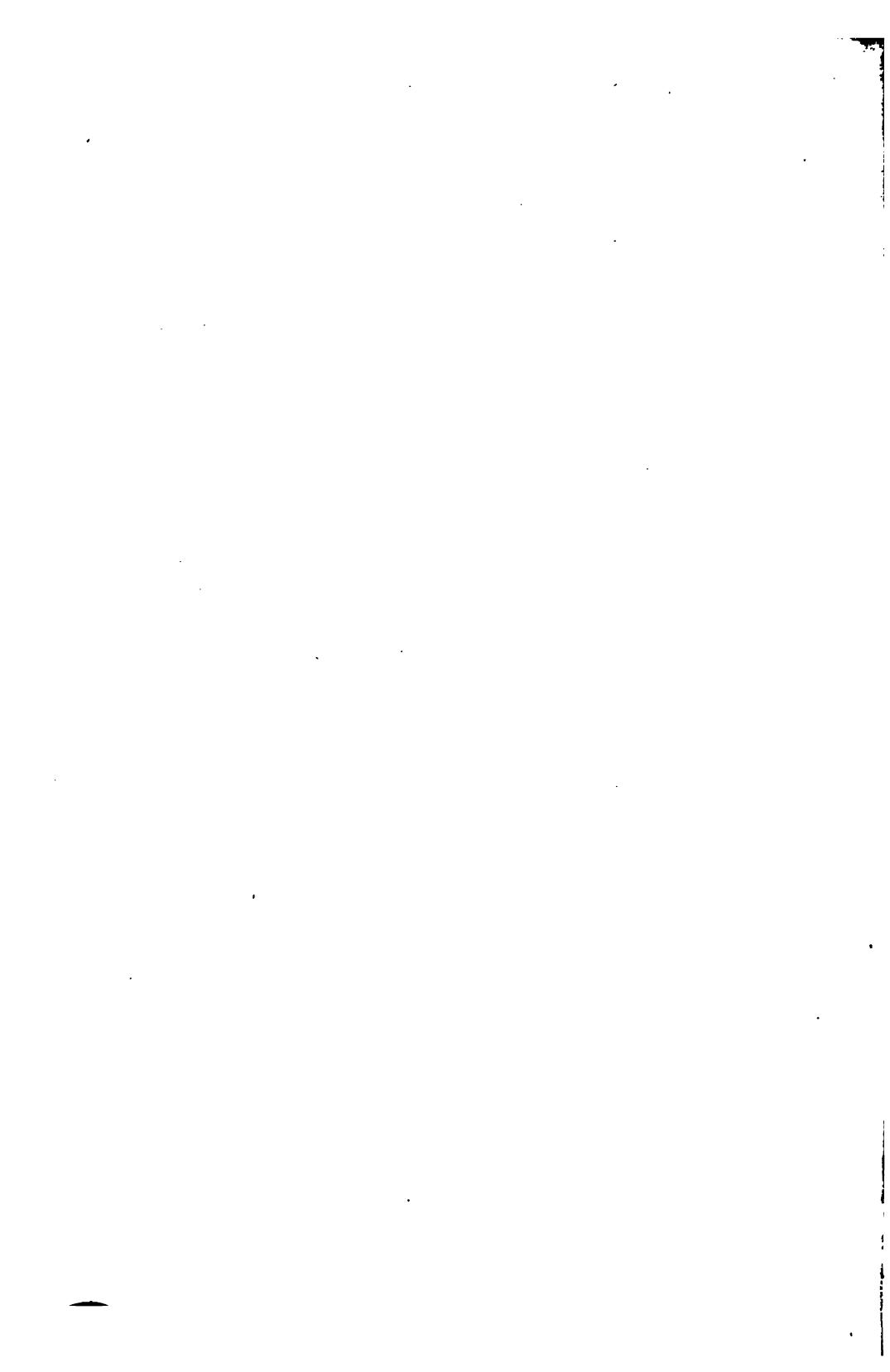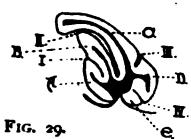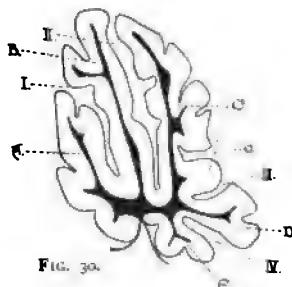
FIG. 39.

FIG. 40.

FIG. 41.

FIG. 42.

FIG. 43.

FIG. 44.

FIG. 45.
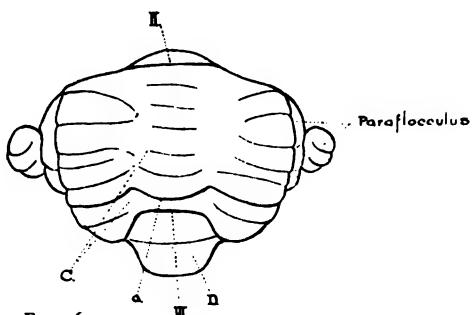
FIG. 46.

Professor O. CHARNOCK BRADLEY on the Development and
Homology of the Mammalian Cerebellar Fissures.
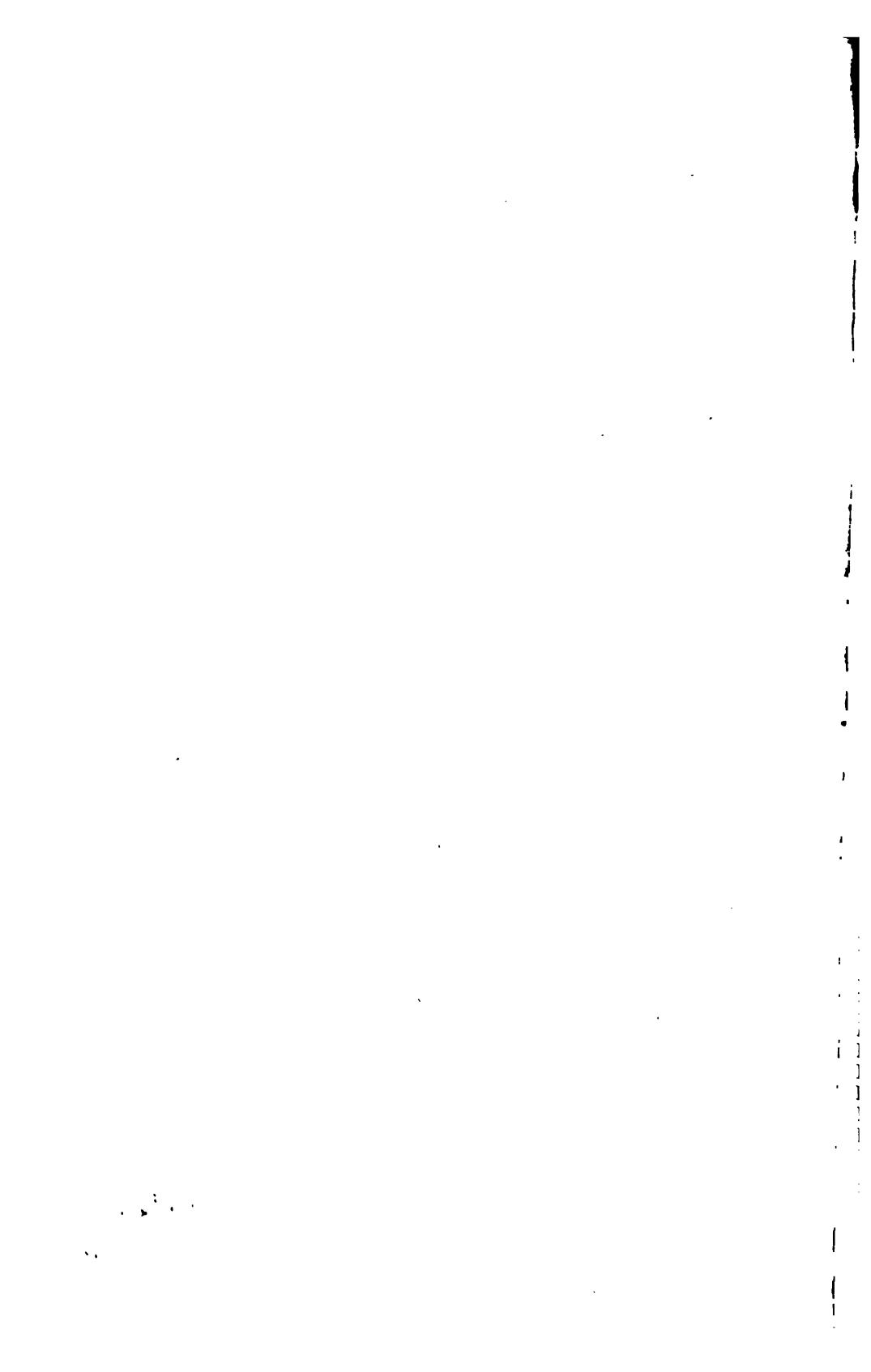
PLATES XII.-XVI.

EXPLANATION OF FIGURES.

In all the figures the same letters and figures are used for corresponding fissures or lobes. The application of the letters and figures is explained in the text.

p.m.v. (in figs. 1 and 3) = posterior medullary velum.

a.m.v. (in figs. 4 and 7) = anterior medullary velum.

ch.pl. (in figs. 1, 2 and 3) = choroid plexus.

All the sections (with the exception of that shown in fig. 2) are in the median plane and sagittal in direction.

Fig. 1. Rabbit embryo, 18 days, 21 mm. Mesial sagittal section through the cerebellar lamina.

Fig. 2. Same embryo. Sagittal section where the cerebellar lamina and the medulla are joining. *lat. rec.* = lateral recess.

Fig. 3. Rabbit embryo, 20 days, 37 mm. Mesial sagittal section through the cerebellar lamina.

Fig. 4. Rabbit embryo, 21 days, 42 mm. Mesial sagittal section.

Fig. 5.   ,,   22 days, 50 mm. Posterior view. × 2.

Fig. 6.   ,,   22 days, 50 mm. Left lateral view. × 2.

Fig. 7.   ,,   22 days, 50 mm. Mesial sagittal section.

Fig. 8.   ,,   23 days, 50 mm. Posterior view. × 2.

Fig. 9.   ,,   23 days, 50 mm. Anterior view. × 2.

Fig. 10.   ,,   23 days, 50 mm. Mesial sagittal section.

Fig. 11.   ,,   55 mm. Mesial sagittal section.

Fig. 12.   ,,   24 days, 59 mm. Mesial sagittal section.

Fig. 13.   ,,   25 days, 64 mm. Posterior view × 2.

Fig. 14.   ,,   25 days, 64 mm. Anterior view. × 2.

Fig. 15.   ,,   25 days, 64 mm. Mesial sagittal section.

Fig. 16.   ,,   27 days, 67 mm. Posterior view. × 2.

Fig. 17.   ,,   27 days, 67 mm. Anterior view. × 2.

Fig. 18.   ,,   27 days, 67 mm. Mesial sagittal section.

Fig. 19.   ,,   28 days (?) 67 mm. Posterior view. × 2.

Fig. 20.   ,,   28 days (?) 67 mm. Anterior view. × 2.

Fig. 21.   ,,   28 days (?) 67 mm. Mesial sagittal section.

Fig. 22. Rabbit, 30 hours after birth. Posterior view. × 2.

Fig. 23.   ,,   30 hours after birth. Anterior view. × 2.

Fig. 24.   ,,   adult. Anterior surface. × 2.

Fig. 25.   ,,   ,,   Left lateral surface. × 2.

Fig. 26.   ,,   ,,   Posterior surface. × 2.

Fig. 27. Lepus timidus. Posterior view. × 2.

Fig. 28. Rabbit, adult. Mesial sagittal section.

Fig. 29. Sorex vulgaris. Mesial sagittal section.

Fig. 30. Erinaceus Europæus. Mesial sagittal section.

Fig. 31.   ,,   ,,   Anterior surface. × 2.

Fig. 32.   ,,   ,,   Left lateral view. × 2.

Fig. 33. Erinaceus Europæus.   Superior view.   × 2.
Fig. 34.   „   „   Posterior view.   × 2.
Fig. 35. Talpa Europæa.   Superior-posterior view.   × 2.
Fig. 36.   „   Anterior surface.   × 2.
Fig. 37.   „   Mesial sagittal section.
Fig. 38. Mus decumanus.   Posterior view.   × 2.
Fig. 39.   „   Superior view.   × 2.
Fig. 40.   „   Anterior surface.   × 2
Fig. 41.   „   Mesial sagittal section.
Fig. 42. Arvicola amphibius.   Superior surface.   × 2.
Fig. 43.   „   „   Anterior surface.   × 2.
Fig. 44.   „   „   Mesial sagittal section.
Fig. 45. Arvicola agrestis.   Mesial sagittal section.
Fig. 46. Pteropus poliocephalus.   Superior view.   × 2.
Fig. 47.   „   „   Posterior view.   × 2.
Fig. 48.   „   „   Anterior surface.   × 2.
Fig. 49.   „   „   Mesial sagittal section.
Fig. 50. Sciurus vulgaris.   Anterior surface.   × 2.
Fig. 51.   „   Superior view.   × 2.
Fig. 52.   „   Posterior view.   × 2.
Fig. 53.   „   Mesial sagittal section.

THE EVOLUTION OF THE TEETH IN THE MAMMALIA.

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OF the many problems in Comparative Odontology, one of the most interesting morphologically and most important phylogenetically is that dealing with the origin of the complex crowns of the mammalian cheek-teeth, and their evolution from a primitive haplodont type. The importance of this problem lies in the fact that the teeth, composed of the hardest tissues in the body, enamel and dentine, have furnished the sole remains of many an ancestral form, at least so far as palæontological evidence exists at the present time. This being so, the gradual evolution of the dental patterns may not unreasonably be expected to throw light upon the origin and inter-relationships of the mammalia. The latter question was one of the subjects for general discussion at the Fourth International Congress of Zoology held in Cambridge in 1899.

By almost unanimous consent the ancestors of the mammalia are to be looked for among the reptilia, though various writers have furnished what might be considered as arguments in favour of a direct amphibian descent.

In 1879 Huxley, in discussing the characters of the mammalian pelvis and the homologies of the abdominal muscles of the monotremata, says (12), " It seems to me that in such a pelvis as that of the Salamandra we have an adequate representation of the type from which all the different modifications which we find in the higher vertebrata may have taken their origin." He also pointed out that the pectoral girdle of the monotremes is "as much amphibian as it is sauropsidan ; the carpus and tarsus of all the Sauropsida, except the Chelonia, are modified away from the Urodele type, while those of the mammal are directly reducible to it."

Professor Marsh (20) also points out that the dicondylian skull is not present in any true reptile, "although the contrary has been asserted. The nearest approach appears to be where

there is a single bifid condyle, cordate in shape, with the two lobes meeting below, as in some reptiles and a few birds, but not separate as in mammals and amphibians." Moreover, Hubrecht has shown that the mammalian ovum approximates more nearly to the amphibian type than to the reptilian. Dr Gadow, on the contrary, considers it beyond reasonable question that the mammals have sprung from some reptilian stock ("the attempts to derive them from amphibia, without the intervention of reptiles, are as gratuitous as they have proved futile") (6).

That the mammals were primitively derived from verte-brates having a general covering of some form of dermal appendage, possibly similar to that of existing elasmobranchs, is, I think, certain. That such appendages partook of the nature of teeth is evidenced by their vaso-dentinal structure in many fossil forms. The earliest adult lung-breathing vertebrates known are the Stegocephala of the Lower Carboniferous of Western Europe. These, as Smith Woodward points out, "exhibit many resemblances to the palæozoic Crossopterygian fishes in the dentition and the outward aspect of the skull" (33). Many of the Crossopterygii were more or less completely covered with dermal appendages, and a "ventral armour of small overlapping scales" is almost universal among them, some being "even armoured dorsally."

In the mammalia the presence of hair or fur over the surface of the body points back to the primitive condition, for, as Huxley says (11), "It appears to me indubitable that the teeth and the hairs are homologous organs."

The balance of evidence therefore tends to show that the mammals were primitively derived from a fish-like precursor, having a general covering of tooth-like appendages. In the course of evolution these underwent various modifications, those retaining the tooth-like characters becoming more restricted in their area of distribution. In existing fishes the latter are by no means limited to the jaws, being present in some of the Teleosteans on all the bones of the mouth, as well as those of the hyoidean and branchial arches. Ascending the vertebrate series, they become yet more restricted, being found only on the maxillæ, pre-maxillæ, mandible, and on the roof of

the mouth (the vomerine teeth of the amphibia), these last tending to disappear in the fossil Theriodontia, and are wanting in most existing reptiles and mammals.

With this gradual limitation in area of distribution, there is a specialisation of the teeth themselves, which at the same time acquire a greater degree of fixity. That the greater specialisation is confined to those animals in the direct line of vertebrate ancestry is not the case, the teeth of the Labyrinthodonta being vastly more complex than those of any mammal. In fishes the teeth are found upon the inner sides as well as upon the free edge of the jaws, and as they become worn down fresh ones take their place, giving rise to a polyphodont condition. Among the reptilia they are usually pleurodont or acrodont in their mode of attachment, though in the crocodilia as in the mammalia the thecodont condition obtains.

The type of the primitive tooth was the haplodont, or simple cone; and the object of the present paper is to endeavour to trace the evolution of the complex crowns of the mammalian cheek-teeth from such a pattern.

Complex teeth are by no means limited to the mammalia, being found in the fishes, amphibia and reptiles. In the earliest sharks complex teeth are present, which have arisen by the fusion of originally separate cusps. In the Cochliodontidæ of the Upper Palæozoic there is believed to have taken place not only a fusion of the teeth of the same series, but also of those of successional series. Other methods of tooth complication have probably been in operation in former geological times. The Notidanidæ of the Jurassic, Cretaceous and Pliocene periods show a progressive addition in the number of cusps, in such a manner as to render the concrescence hypothesis highly improbable. Again, in existing fishes, Semon (25) has shown that a fusion of individual cusps takes place in the teeth of Ceratodus; and Professor Graham Kerr tells me that he has been able to verify this statement, though he has not been able to find any traces of concrescence in Lepidosiren. Again, in the reptilia, though a homodont dentition of a haplodont type is the rule, nevertheless in the existing Sphenodon and in many of the Permian and Triassic forms, a heterodont condition is to be

found. Harrison has shown (10) that in the development of the teeth in Sphenodon there are distinct evidences of concrescence. Among recent mammals, while complex cheek-teeth are almost universal, the haplodont exists in such forms as Delphinus.

Various theories have been advanced from time to time to account for the evolution of the mammalian molars from this simple pattern. Most of these are too well known to need description; reference will therefore only be made to them for the purposes of criticism.

The first attempt at a systematic description of the teeth of mammals was made by Cuvier (3) in 1825. Subsequently Owen took up the study and added considerably to our knowledge. As far as I have been able to ascertain, the first writer to advance any theory in explanation of the molar evolution was Gervais (8) in 1854. His theory was practically that now known as the Concrescence theory, which supposes the fusion of a number of reptilian cones, the apices of which would give rise to the various cusps of the mammalian molars. Other investigators followed in the same lines, notably Gaudry (7) in 1878, and Dybowski (4) in 1889. Though these writers suggest this theory as applicable to the molars of mammals in general, they were more particularly concerned with those of the ungulata and proboscidea. Among more recent writers Röse claims to have seen cusps in the process of fusion in the teeth of the chameleon (23), and Kükenthal in the rudimentary molars of the walrus (14). The latter author also regards as an argument in favour of this view the fact that in the cetacea the teeth disintegrate by a splitting down between the cusps, a reverse process to that of evolution. He also cites the multituberculata as having teeth probably formed by the fusion of teeth, not only of the same dentition, but of those of different dentitions, thus accounting for the transverse rows of three cusps so frequently found in these mesozoic forms, while the molars of the higher mammals, with their transverse rows of two cusps, he would regard as representing a fusion of the milk and permanent dentitions. As far as I am aware, this theory has not been adopted to account for the complexity of the premolars, except by inference they may be held to represent an anteroposterior fusion of cusps of a single dentition.

M. F. Woodward (31) adversely criticises these conclusions from an embryological standpoint.   He says this view "will not hold for all mammals, for if the lingual continuation of the dental lamina represents the anlage of the replacing teeth, that structure can be seen in some mammals to remain quite distinct from the adult molar, and in the end to gradually disintegrate as the growth energy is abstracted from it by the larger and earlier developed tooth."   Anyone who has had practical experience in the investigation of tooth-genesis will readily admit the truth of Woodward's statement.

In earlier papers I was unable to admit the validity of the concrescence hypothesis ; more recently, however, I have been induced to accept it, but not to the full extent advocated by Kükenthal and others.   An antero-posterior fusion of the teeth of the same dentition appears to me now to be the only solution of the difficulty in accounting for the duplex condition of the true molars of the greater number of mammals and of the complex cheek-teeth of the rodents and fossil multituberculata. The repetition, so to say, of the development of the anterior and posterior halves of the rodent molars seems to me to render this highly probable, though I have not yet seen any actual fusion of enamel germs.   It may quite well be that this early stage may have become slurred over in the recapitulatory history, until it is entirely lost at the present day.   Possibly the same may be true of the ungulates and proboscidians.

Kükenthal's adaptation of this hypothesis to the molars of the higher mammals, in so far as it relates to the fusion of teeth of different dentitions, is, I think, untenable.   The quotation from Woodward just given sufficiently disposes of the lingual downgrowths of the dental lamina, and the same remark applies with equal force to the labial downgrowths, where these are distinct and do not take part in the formation of an external cingulum, many instances of which are known to occur.   In the concentric epithelial bodies of Cavia, Canis, Gymnura and Ornithorynchus we have, I believe, the last traces of a vanishing dentition which must have preceded the cheek-teeth on account of their labial position.   These bodies remain quite distinct from the teeth themselves, and show no tendency to become fused.

Little or no weight attaches to the evidence derived from the disintegration process of the cetacean molars. That there is nothing inherently improbable in the Concrescence theory is true; indeed, the shortening of the jaws which occurs so generally throughout the mammalia might easily account for antero-posterior fusion, though it is difficult to conceive of any forces which would produce lateral fusion of successive dentition.

That fusion does take place in the teeth of other vertebrates has already been shown. Nor must the evidence furnished by Ameghino be omitted, the numerical relationships between the cusps of the mammalian teeth and the number of individual teeth being very striking (1).

From a consideration of the facts available, I am inclined to accept the Concrescence theory in so far as it relates to an antero-posterior fusion of the cusps in the true molar region only, but I am at present unable to find sufficient evidence of any lateral fusion in these or other forms.

The Tritubercular theory was advanced by Cope in 1873 (2). It has since become the most widely known theory of mammalian tooth-genesis, owing to the numerous publications on the subject by H. F. Osborn, Scott, Earle, Allen, Wortman, and other American morphologists. It has also met with wide acceptance on the European continent, finding adherents in v. Zittel, Rutimeyer and Schlosser. Röse, Leche and Taeker have dealt with the subject from the embryological standpoint, and would appear to have accepted it, though somewhat more reservedly. In this country the theory has not met with such general acceptance. Sir William Flower and Lydekker appear to have done so; but with the majority of English writers, including Forsyth-Major, Smith Woodward, M. F. Woodward and E. S. Goodrich, trituberculism seems to have found but little favour.

The discussion as to the tenability of this hypothesis can be approached from two points of view, the embryological and palæontological.

The tooth-genesis has been worked out in individual members of quite a number of mammalian orders, attention being paid to the order of cusp development. Röse has dealt with the

primates (21) and marsupials (22), Taeker with the ungulates (26), and I have investigated the tooth-genesis in the carnivores (27), rodents (28), and recently in man, while M. F. Woodward has examined the insectivores (32). The results exhibit a remarkable uniformity. With the exception of two insectivores, Centetes and Ericulus, in no single instance does the protocone develop first, as it should do if ontogeny in any way recapitulates phylogeny ; with these two exceptions, the paracone and protoconid, in other words the antero-external cone, being always the first to appear. This remarkable uniformity cannot be a mere coincidence, and can, I think, only lead to one conclusion, namely, that the paracone and protoconid are homologous cusps, and represent the primitive reptilian cone, as first suggested by Röse (21); as far as I am able to understand Winge (30), this is the conclusion at which he also has arrived. As to the exceptional insectivores above alluded to, Centetes and Ericulus, the protocone of the molars is said to develop first. This cusp is so named from a tritubercular standpoint, but it appears open to doubt whether it is in reality the homologue of the protocone of most other mammals. If the teeth of these two forms be examined, it will be seen that the so-called paracone and metacone are placed externally to the protocone, and would seem to partake of the nature of external cingulum cusps, such as one finds highly developed in Otocyon among the carnivores, and Talpa and Chrysochloris among the insectivores. Of the three last mentioned animals, in Talpa alone has the tooth-genesis been worked out, and in it the paracone is the first to appear. A comparison of the molars of Talpa and Centetes leads me to believe that the so-called protocone of the latter is really the homologue of the paracone of the former, a conclusion entirely in agreement with Woodward, and a modification of the view put forward by Mivart in 1868 (15), but a conclusion not hitherto usually accepted. Should this interpretation prove to be correct, then all the insectivore molars fall into line with those of other mammals as yet embryologically investigated.

It has been necessary to dwell upon this point at some length since Prof. Osborn, in a memorial paper to the late Prof. Cope, entitled " Trituberculy " (17), finds in Woodward's work on the

tooth-genesis in the insectivores further evidence in favour of this theory. Professor Osborn quotes from the first part of Woodward's work, dealing with the order of cusp development of Centetes and Chrysochloris, in which the so-called protocone is said to arise first, but he omits to mention that Woodward is later on concerned at some length with the discussion as to the homology of the protocone in these forms with the paracone of other insectivora, and in which he says (p. 588)—"With regard to the tritubercular upper molar of the Centetidæ, I should conclude that the main cone of this type of tooth, usually termed the protocone, was really the paracone"; and he further distinctly states in the recapitulation of his conclusions that "the antero-external cone, or paracone above and the protoconid below, is the primitive cone both in the molars and premolars." Consequently, the inference drawn by Osborn from the insectivora is not in accord with Woodward's own conclusions, which were entirely opposed to the Cope-Osborn theory.

Again, I have previously shown (27) that in d.pm. 4 of the dog and m. 1 of such a form as *Cyon rutilans* the protocone is non-existent. I also adduced several other reasons derived from embryology and comparative morphology which appear to me to militate against the tritubercular theory. Moreover, palæontology, upon which the upholders of this view mainly rely, appears to me singularly deficient. In the first place, the fossil forms are mainly known by the lower jaws only, and yet it is generally agreed that the teeth of the upper jaw are those which retain the most primitive characters.

The majority of these fossils have been found in the same strata, and the evidence that the phylogenetic sequence is that adopted by the upholders of the tritubercular theory appears to be extremely hypothetical. I have in former papers entered more into detail on this point; it is therefore unnecessary to recapitulate, but I am of the opinion that the palæontological evidence is as deficient as the embryological is damaging, and the absence of all proof in favour of the supposed rotation of the cusps, which is the very foundation of the theory, is an insuperable difficulty, at least in the present state of knowledge.

The Multituberculate theory, suggested by Forsyth-Major in (5) 1893 to account for the evolution of the rodent molars

has met with but scanty recognition. That this theory can apply to the premolars of such orders as marsupials, carnivores, insectivores and primates, with their full numerical dentitions, is scarcely possible. With the objections to the adoption of such a view I have dealt elsewhere (27), with the reservation that it might apply to the monotremes, rodents and ungulates. Since then I have worked out the tooth-genesis in the rodentia, and have concluded that for them a multituberculate origin should be admitted. Taeker's work on the tooth-genesis of the ungulates would appear to lead to a different result, and it would be interesting to reinvestigate the matter in the light of more recent discoveries.

Having thus briefly passed in review the more important hypotheses as to the molar and premolar evolution, and being unable to conclude that any one of them is satisfactory, I venture to advance a new theory which seems to me to be nearer to a correct interpretation of the known facts.

This hypothesis is based on the importance, in the production and development of cusps, of the cingulum. That this is an extremely archaic structure is indisputable, being well marked in the Anomodontia, for example Nythosaurus. Moreover, in the early development of the teeth of existing mammals it is proportionately very large. In the primitive reptilian condition it would appear to have *surrounded* the base of the primitive haplodont cone, but in the process of evolution that portion of the cingulum to the outer side of the primary cone, the external cingulum, has disappeared to a considerable extent in the majority of mammals, though its position may generally be noted by the presence of a slight longitudinal rounded elevation. The ends of the internal cingulum give rise to small anterior and posterior cusps, a triconodont tooth, such as is found in the Triassic Dromatherium Amphilestes and Microconodon, and in the premolars of *Amphitherium Prevostii* of the Stonesfield Slate, as described by Owen (19) and Goodrich (9). A precisely similar type of tooth is to be seen in the milk incisors of the dog, as previously figured (27). With an increase in size of these anterior and posterior cusps, a tooth with three sub-equal cusps in the same longitudinal row would be produced, such as exists in the fossil Triconodon and in the premolars of the existing

felidæ (fig. 1 and fig. 2B). The origin of these and other cusps and their subsequent growth is probably due to mechanical causes.

In the course of the further evolution and specialisation of

FIG. 1.—Upper third premolar of Hyæna. External aspect, showing external cingulum and small anterior and posterior cingulum cusps. (Mus. Zool. Univ. Camb.)

the cheek-teeth there is a tendency in some forms to a disappearance of the anterior cingulum-cusp, as in the upper carnassial of the dog and bear (fig. 2A), while in the tiger both anterior

FIG. 2A.—Upper fourth premolar of *Canis familiaris*, with external cingulum and posterior cingulum cusp only. (Mus. Zool. Univ. Camb.)

FIG. 2B.—Upper fourth premolar of *Felis tigris*, with external cingulum, and enormously developed anterior and posterior cingulum cusps. (Mus. Zool. Univ. Camb.)

and posterior cingulum cusps are very large. The anterior is present and of large size in the lower carnassial of Ursus and Meles; it is proportionally smaller in Lutra, Herpestes and Canis, while in Felis it is altogether absent. The so-called protocone of the premolars, where it exists, can be seen to rest upon the internal cingulum; it is in fact an internal cingulum-cusp, developed by mechanical agencies; where that cingulum has disappeared or almost so, no protocone is to be found,

as for example in pm. 4 of *Cyon rutilans* and the anterior premolars of most mammals.

The external cingulum usually disappears, leaving only a slight longitudinal elevation along the outer side of the tooth to indicate its position; but in Peralestes, Otocyon and the Centetidæ, not only does the external cingulum persist, but it gives rise to well marked cusps. The cause of this is difficult to understand. It has been suggested (32) as being "of use to insect-feeding animals," but this would not apply to the carnivorous Otocyon; and since this condition is absent in the majority of the insectivora, the suggestion would not appear to be very felicitous. Again, it cannot be due to the mechanical stimulation caused by the interlocking of the teeth in closure of the jaws, as external cingulum-cusps in these animals are equally pronounced in both upper and lower teeth.

Thus far there is an accordance between this theory and the embryological and palæontological evidence as to the evolution of the mammalian premolars, the paracone representing the reptilian haplodont tooth, and being the first to develop in the teeth of all forms hitherto examined. Moreover, Scott has shown (24) from a comparison of fossil forms that this cone is the primitive one phylogenetically.

The question now presents itself—Do the molars develop along the same lines as the premolars? Scott (*loc. cit.*), from a consideration of the palæontological evidence only, concludes that they do not. This conclusion appears at first sight to be at variance with embryological results.

In attempting to outline the developmental history of the true molars, it may be well to begin with a consideration of the conditions present in the rodentia. These teeth first appear in the form of a simple cone surrounded by a cingulum, of which the external and internal parts are the most pronounced. The primary cone ultimately gives rise to the antero-external portion of the adult tooth, which may therefore on morphological grounds be regarded as the paracone, though the individual cusps disappear from the tooth even before it is erupted. The tooth-germ grows in such a manner as to give rise to a posterior half, similar to but smaller than the anterior; there is, in fact, an antero-posterior reduplication. In this, presumptive evidence is

afforded in favour of concrescence, though I have never yet
actually observed the fusion of two separate enamel-germs;
nevertheless it is quite possible that in such primitive forms as
the rodents, dating back almost unchanged to the Lower Eocene
period, the early stages in the tooth-genesis may have become
abbreviated.

The rodent molars, according to the hypothesis under con-
sideration, represent a simple ancestral type, in which two
primary cones, with their internal and external cingula, have
become fused, the external lasting only for a time, and disappear-
ing before the tooth has erupted. The molars of the greater
number of rodents seem to be derived from the fusion of two
primitive cones only, but in exceptional cases, as for example
Arvicola amphibius, it might be inferred, judging from the adult
teeth, that four were originally involved, while, as an intermediate
condition, the posterior upper molars of Mus and Cricetus and
the posterior tooth in the mandibular ramus of *Gerbillus indicus*
give evidence of the concrescence of three primary cones. It
would be extremely instructive to investigate the tooth-genesis
in such forms.

In the Multituberculata, which, agreeing with Forsyth-Major,
I regard as the precursors of the rodentia (1), there appears,
according to this hypothesis, to be a fusion of the same primitive
type of tooth, but in these, as might be expected, the external
cingulum has not yet aborted in the majority of forms, though
the process has already commenced in some of the Polymasto-
dontidæ, for example *P. tabensis*, and in m. 2 of Meniscoessus (18).
The further complication in existing rodents is due to the
involutions of the enamel, whereas in the multituberculata this
does not exist, the greater complexity of tooth-pattern being
brought about by increase in the number of teeth which have
become fused. The number of such teeth so involved seems to
vary in different cases. In *Ctenacodon potens* there appear to
be four, while in *Polymastodon attenuatus* there are at least
seven or eight. Thus the so-called true molars of the Rodentia
and Multituberculata conform to the same general type as the
premolars of the other Eutheria, the tendency likewise being the
suppression of the external cingulum; the difference being that
in the premolars the anterior and posterior cusps are develop-

ments of the anterior and posterior portions respectively of the surrounding cingulum; in the molars an antero-posterior fusion of originally separate teeth has led to the suppression of these parts and given rise to the multituberculate pattern.

From a comparison of Taeker's account of the development of the ungulate molar (26) with that of my own researches in the Caviidæ, the hypothesis under consideration would seem to me to be capable of similar application. In the majority of ungulates the molars might also be produced by the fusion of two originally distinct teeth. Such a primitive type with but little further complication is to be observed in the unworn molars of Anchitherium from the Lower Eocene (fig. 3B), while the corresponding unused teeth of the existing horse show but slight further changes,

FIG. 3A.—Crown surface of upper first molar of *Cyon rutilans*.   (Zool. Mus. Roy. Coll. Sci. Lond.)
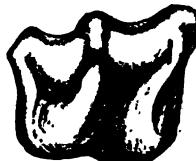
FIG. 3B.—Crown surface of unworn molar of *Anchitherium*.   (After Flower and Lydekker.)

except in the increased size and development of the internal cingulum. Comparison of these teeth with those of the rodents Cavia and Lepus present a general similarity in type, though in the latter forms the teeth have become much more compressed antero-posteriorly. The increased complexity of the cheek-teeth of the rodent Muridæ, caused by enamel involution, finds analogy in the teeth of that extremely interesting form *Hyrax capensis* and in those of the rhinoceros, while the more bunodont molars of the Suidæ are comparable to those of the unworn teeth of the Hystricidæ. The pattern of tooth found in the Bovidæ and Cervidæ would not appear to find any expression among rodent types, but the mode of their evolution seems to

run on parallel lines with that of the more complex teeth of the carnivora, as exemplified by *Canis aureus* (fig. 4), and to which subsequent reference will be made.

In the molars of the Proboscidea we find analogy between the

Fig. 4A.—Crown surface of molar and premolar of *Nemorhadus goral*. (Mus. Zool. Univ. Camb.)

Fig. 4B.—Crown surface of upper first molar of *Canis aureus*. (Zool. Mus. Roy. Coll. Sci. Lond.)

teeth of the fossil Polymastodon and existing Caviidæ and Leporidæ; fusion of a number of teeth with considerable antero-posterior compression, but no further complication due
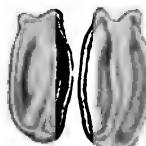
Fig. 5A.—Crown surface of molar teeth of Rabbit. × 4. (Mus. Zool. Univ. Camb.)
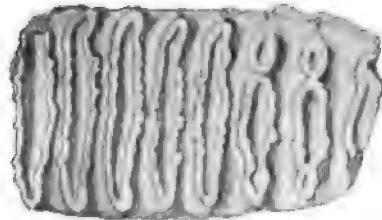
Fig. 5B.—Crown surface of molar tooth of *Elephas antiquus*, from the Cambridge Gravel. × ½. (Mus. Zool. Univ. Camb.)

to the production of cingulum-cusps or infoldings of enamel. The well known molars of the Elephant and Mastodon (fig. 5B)

have numerous transverse ridges grouped in pairs, each of which might be regarded as representing the complete cingulum of an originally separate tooth, longitudinally compressed, and considerably elongated in the transverse axis.

Viewing the molar genesis in the dog in the light of the knowledge obtained from the rodents, the same interpretation seems justifiable. The condition obtaining in the premolars of the carnivora is simple on the cingulum-cusp hypothesis, but its application to the molars offered greater obstacles. The two main external cones might be so explained, were it not for the fact that distinct and well marked anterior and posterior cingula were also present. By admitting the antero-posterior fusion of separate haplodont cones of the same series with their cingula, the difficulties appear to me to vanish. The two main external cones of the molars so general throughout the mammalia represent two originally separate haplodont teeth, the opposed cingula being fused, and giving rise to the tooth substance between the main cones, the anterior cingulum of the anterior and the posterior cingulum of the posterior moiety persisting as the corresponding parts of the adult tooth. By the interlocking of the longitudinal series of cusps in the teeth of the upper and lower jaws, the internal cingula have been wedged inwards, forming a more transversely elongated tooth, which would correspondingly produce a more efficient crushing surface. Such a simple form of tooth is to be seen in Perameles, Perigale, and a number of other marsupials, as well as in the primitive molar of *Cyon rutilans* (fig. 3A). Accompanying the increased severance of the internal cingulum from the primary cones in a mesial direction, there is a gradual addition in the number of cusps, all of which become developed in the intervening space, the production of such being doubtless due to the mechanical stimulation when the teeth of the opposing jaws are brought into contact. Among the dogs this is carried to an extreme in the molars of the jackal (*Canis aureus*) (fig. 4B).

It is unnecessary to press this point further in its application to the other mammalian orders. Suffice it to say that I have dealt with what I conceive to be the most difficult of interpretation, the teeth of the Insectivora, Cheiroptera and Primates offering no special obstacles.

We must now revert once more to the question raised by Scott: Do the molars and premolars follow the same line of evolution? The answer to be given from the foregoing considerations is that they do in so far as the early stages are concerned, but that in the later stages of the developmental history they diverge. In the premolars there is no sufficient evidence of concrescence, but they specialise along their own lines in the growth of the cingulum and the production upon it of secondary cusps, principally anteriorly and posteriorly, though the addition of cusps upon the internal and more rarely external cingulum takes place. In the molars the complexity of tooth pattern is chiefly due to the longitudinal fusion of primitively simple teeth, further complications such as those produced by involutions of the enamel being quite secondary, and developed within the limits of individual groups. Such a conclusion raises further minor points, which must not be omitted. (1) If the two main external cones of the molars represent two teeth of the same series, and are therefore, so to speak, of equal phylogenetic value, how comes it that in all the published results of investigations into tooth-genesis the anterior cone develops first in point of time, and is therefore of prime ontogenetic value? To this I would answer, that it is in accord with the recognised fact that the molars develop in succession from before backwards, the posterior 'wisdom' teeth being the last to appear. The order of evolution would therefore be first the paracone, then the metacone of m. 1, next the paracone of m. 2, followed by its corresponding metacone, and so throughout the series.

(2) In view of the above conclusion, what interpretation is to be placed upon the teeth usually regarded as premolars, found in certain of the multituberculata; instance the three lower posterior premolars of *Plagiaulax minor*? I have elsewhere (29) thrown doubt upon the validity of the generally accepted distinction between molars and premolars; but assuming it to be correct, Smith Woodward asserts (33) that in Plagiaulax "nothing is known of the mode of succession, but these teeth are usually termed premolars." Presumably, the reason is to be found in an attempt to harmonise the dental formulæ—4 premolars and 2 molars—with that of recent mammals. This is unnecessary,

since Osborn has shown (16) in his paper " On the Structure and Classification of Mesozoic Mammalia " that the dental formula of the primitive heterodont mammal should be considered as i. 4, c. 1, pm. 4, m. 8.   In my opinion the three posterior premolars of Plagiaulax partake much more of the molar pattern, and I would certainly be disposed to regard them as such.   The anterior premolar is too much reduced to express any definite opinion.

(3) If the entire molar tooth has been evolved from the fusion of teeth of the same series, as suggested, what has been the fate of the preceding milk dentition ?   It has been mentioned already that the advocates of concrescence 'per se' regard the molars as the result of the fusion of teeth of three different series.

The presence of concentric epithelial bodies, such as occur in Canis, Gymnura and Ornithorhynchus, seems entirely against the view of the milk teeth forming the outer portion of the functional molars.   Now, it is well known that the deciduous teeth develop slightly in front and to the outer side of their successors.   It may be readily conceived that in an antero-posterior fusion such as above described the milk series would have little or no room to develop, while the larger and more functional the molars became the more they would withdraw nourishment, and thus doubly tend to prevent the teeth of the deciduous dentition coming to perfection.

Lastly, two other questions suggest themselves : What factors have caused the fusion in the molar region and not in the premolar, and why have the latter departed on a special line of evolution ?   Shortening of the jaws has probably been the principal factor, acting mainly on the posterior end of the bone, coupled with the larger size and number of the teeth in this situation; whereas, in the premolar region, the teeth are fewer in number, and the early loss of some in many animals causing a diastema, does not tend to produce so much crowding, and permits of a greater longitudinal growth of the individual teeth, in adaptation to the different physiological requirements.

It is impossible within reasonable limits to discuss the application of this hypothesis at any great length in reference to all the mammalian orders.   Sufficient has, I hope, been

stated to fully explain the underlying idea as to mammalian tooth-genesis; and though there may be difficulties as to its adaptation in every instance, it would appear to me more capable of universal application, both to recent and extinct forms, than any of the theories previously suggested, and at the same time to be more in accordance with the known facts of embryology and palæontology.

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THE FORM OF THE DILATED CEREBRAL VENTRICLES IN CHRONIC BRAIN ATROPHY. By J. O. WAKELIN BARRATT, M.D. Lond., F.R.C.S. Eng., *Pathologist to the West Riding Asylum, Wakefield.*

WHEN chronic wasting of the cerebrum occurs, the atrophy of the gyri, with corresponding widening of the sulci and distension of the pia-arachnoid with fluid, forms a striking appearance when the brain before removal is viewed *in sitú* from above, but the accompanying ventricular dilatation in such cases is less readily studied, because the form of the ventricles is altered as the brain is cut up in order to bring these cavities into view. The wasting of brain tissue may be due to a disappearance of whole neurons, or merely of nerve-cell processes, the extent to which these two degenerations occur in individual cases being as yet imperfectly ascertained. The bulk of the axis-cylinders and their offshoots, with their myelin sheaths, and that of the corresponding protoplasmic extensions, taken together, must frequently if not generally exceed that of the cell-bodies, so that the atrophy may in some cases be much more due to disappearance of the former than of the latter. The wasting of cerebral gyri is due to both forms, that is, atrophy of cell-bodies and of cell-processes. The enlargement of the lateral and to a less extent of the third ventricles is, however, due essentially to an atrophy of the thick masses of white substance which come into relation with these cávities. It would naturally follow that if, in a wasted cerebrum, atrophy largely preponderated in particular situations, say in the frontal lobes, such atrophy would be indicated by a disproportionate enlargement of a corresponding portion of the ventricular space; and similarly, atrophy elsewhere would produce correlated local ventricular dilatation. With a view of studying more fully the general form of the ventricular dilatation occurring in chronic brain atrophy, and further, of ascertaining whether any such disproportionate wasting of white matter, as evidenced

by enlargement of the ventricular cavity, occurs, the following investigation was undertaken.

In order better to study the form of the dilated ventricles, plaster casts of these cavities were prepared. In taking out the brain, great care was necessary to avoid altering its shape. As soon as the brain was removed from the skull, the mesencephalon was cut across at its junction with the pons Varolii, and the cerebrum placed in a saturated solution of bichromate of potassium, to which 5 per cent. of formol was sometimes but not always added. In this liquid the cerebrum at first floated, subsequently gradually sinking as it became penetrated by the hardening fluid. During removal a certain amount of fluid necessarily escaped from the ventricles. To avoid the accompanying alteration in size and shape of the ventricular cavity which this entails, some of the bichromate solution was injected into the ventricles through a glass nozzle inserted into the aqueduct of Sylvius, and the injection was continued until some of the fluid returned again through the aqueduct. By this method the shape of the cerebrum and its ventricles was preserved with the least possible alteration.

At the end of from three weeks to two months the brain was sufficiently hardened. It was then placed with the frontal lobes directed downwards and the occipital lobes upwards. The occipital lobes were now sliced off from above downwards until the tips of the posterior cornua were reached. Small openings being made into these horns in order to permit the passage of fluid through them, plaster of Paris was then injected into the aqueduct of Sylvius until it welled up through the minute openings in the apices of the posterior cornua just referred to. It was necessary to repeat the injection many times, in consequence of the dilution of the plaster of Paris with the fluid already present in the ventricles. As soon as the plaster of Paris commenced to set, the orifice of the aqueduct was closed, and when setting was completed, the brain substance was cut away bit by bit. Great care is required to avoid breaking the cast, especially in removing the septum lucidum. More often than not, however, fracture occurs at the foramen of Monro, but this is not of great consequence, as, from the irregular shape of the broken surfaces, reunion can be effected without

any alteration of the relation of the fragments. A cast of the fourth ventricle cannot satisfactorily be made, owing to the escape of plaster into the meshes of the pia-arachnoid by the foramen of Magendie and the openings in the lateral recesses.

When a cast of the cerebral ventricles has been made in this way, the brain itself is necessarily destroyed in the process, so that relation of the form of the ventricular cavity to that of the cerebrum cannot be observed. This difficulty can in part be avoided by making thick frontal sections, placing them together, having previously made sketches of the cut surfaces to scale, and then making a cast. In this way a record both of the form of the ventricles and of their form-relations to the cerebrum is obtained. It is, however, more convenient to study the two separately.

The number of casts of the cerebral ventricles upon which the present observations are based is six. Of these, four were from cases of dementia occurring in patients whose ages at death ranged from 68 to 77 years, and two were from cases of general paralysis of the insane, aged respectively 51 and 55 years.

The dilated ventricular space of the cerebrum consists of three parts, corresponding to the lateral and third ventricles (figs. 1 to 4). Of these, the two former, which are approximately but not accurately symmetrical in shape, are situated on each side of the mesial sagittal plane of the skull, and consist of a body flattened obliquely from above downwards, its inner being lower than its outer border, and three large processes known as the anterior, posterior and inferior cornua, the first arising from the anterior extremity of the body and the two last from its posterior end. The anterior and posterior cornua are flattened from side to side, while the inferior cornua are flattened from above downwards. The anterior cornua are separated from each other by a narrow, the posterior cornua by a wide interval; the inferior cornua, which at their origin curve outwards, turn inwards as they approach their terminations, and thus form a concavity on each side of the mesial plane (fig. 3B).

The cavity of the third ventricle lies within the thalamencephalon and is connected on each side by a narrow neck with

the lateral ventricles at the junction of body and anterior horn.

In its division into three parts the dilated cerebral ventricular space occurring in brain atrophy resembles the normal ventricular cavity,[1] but here the resemblance ceases, for both in its large size and still more in its shape the former diverges from the latter. This divergence is greater the larger the dilatation, and affects not only the general form of the ventricular space, but involves also in varying degree that of each of its divisions.

The six ventricular cavities examined vary much in size and also in form. The smallest (figs. 1A, 1B) approaches most nearly to the form and dimensions of the normal ventricles,
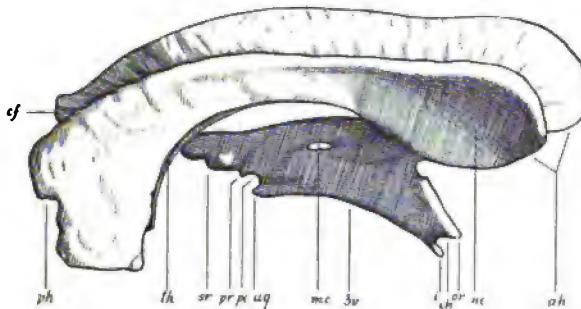
FIG. 1A.

Fig. 1A. Cast of the ventricles of the cerebrum, seen from the right side. Case 1. Male, aged 68 years, suffering from dementia. The ventricular cavity is moderately dilated, so that the lateral ventricles approach the expanded scale-like character of the undilated lateral ventricular spaces, and the third ventricle presents some resemblance to the slit-like cavity exhibited in a normal brain. The lateral ventricles are not perfectly symmetrical, the left anterior cornu, a.h., projecting more forward than the right. The inferior cornua are not present, the cavity of these horns being in part obliterated, through their upper and lower surfaces coming in contact posteriorly. The posterior horns, p.h., are short, almost sessile, and are directed a little outwards. Each is deeply grooved on its inner surface by the calcar avis, c.f. The details of structure are described in the text.

This and the following sketches are of the natural size.

while the others diverge therefrom in proportion to their size. This divergence affects the lateral ventricles far more than the third, which, while it increases in its lateral dimensions, is other-

[1] Cp. "The Form and Form-relations of the Human Ventricular Cavity," *Journ. of Anat. and Physiol.*, vol. xxxvi. pp. 106–126, 1902.

wise but little altered in aspect (cp. figs. 1A and 4). The descending horns are not always represented in the casts (figs. 1 and 2). This arises from the circumstance that the inferior cornua are flattened from above downwards, the upper and lower surfaces of their lining membrane approaching each other or actually coming into contact over a portion of their extent. Perhaps this may be partly caused by the brain being floated with its lower surface upwards in the hardening fluid, when the temporal lobes tend to become flattened, but it is probably due chiefly to the form the brain assumes during life when, in consequence of the lesser specific gravity of the ventricular fluid (1·006) as compared with that of the brain substance (1·038), the inferior cornua tend to become pressed upon from above. In most of the cases (four out of six) the right inferior horn was larger than the left (cp. figs. 2A, 2B, 3A, 3B).

The flattening of the bodies and cornua of the lateral ventricles becomes less marked the greater the dilatation of these cavities. Figs. 1 to 4, which represent a series of ventricular spaces arranged in progressive order and all drawn to the same scale, illustrate this point. The anterior cornua and bodies of the lateral ventricular cavities are the first to lose the strongly flattened character peculiar to the undilated condition ; the loss, though marked, is less conspicuous in the posterior and inferior cornua. The third ventricular space also broadens out from side to side as the general ventricular space enlarges, but this increase in size is not in the same proportion as that of the lateral ventricular space, as the figures indicate.

Asymmetry of the two lateral ventricles is noted in every ventricular space examined. It is not, however, extreme in degree. It affects the bodies (cp. fig. 1B) less than the cornua ; of the latter, the anterior cornua are but little affected, the inferior cornua are more decidedly unequal, and the posterior cornua, except in the first case (figs. 1A, 1B), are markedly asymmetrical.

The six ventricular cavities examined preserve a resemblance in general form sufficient to permit of their being arranged in a graduated series, which corresponds also to their increase in size. The change of form from the flattened character of the normal to the expanded type of the considerably dilated ven-

tricular space is best seen in the bodies and anterior cornua, and to a less extent in the inferior cornua. In the posterior cornua, however, there is, as the figures indicate, so much difference in form exhibited that no such gradation is recognisable. Thus in two cases (figs. 2A, 2B and 4) the tips of the posterior horns are directed inwards, the right in each case more than the left, while in two other cases (figs. 1A, 1B, 3A and 3B) no such incurving occurs, the posterior horns being short and stumpy. There is, therefore, in the case of the posterior cornua, not only lateral asymmetry in the individual ventricular spaces

FIG. 1B.

Fig. 1B. The same cast as exhibited in fig. 1A., seen from above. In addition to the inequality of the lateral ventricles referred to above, it is seen that the septum lucidum, *s.l.*, is displaced to the right in part of its extent above. The upper surfaces of the lateral ventricles are flattened from side to side, and exhibit some degree of transverse furrowing opposite the corpus callosum, especially in front and behind.

studied, but also serial asymmetry. Careful comparison of one with another has failed to furnish me with any suggestion as to the significance of this variation of form in different cases.

The third ventricle does not vary very much in form. Its length from before backwards depends in part upon the extent to which the supra-pineal recess, *s.r.*, is developed. The obliquity and curvature of this portion of the ventricular space of the cerebrum is altered as dilatation occurs (cp. fig. 1A with fig. 4). This appears to be due to the corpus callosum becoming raised

as dilatation occurs, and carrying with it the posterior extremity of the third ventricle, while the anterior and inferior angle preserves its position unaltered or descends a little.

The lateral ventricles are, as already stated, of nearly equal dimensions. In two cases (figs. 3 and 4) the right lateral ventricle was slightly larger than the left; the other two (figs. 1 and 2) were little different in size. The increase in size which the lateral ventricles undergo as the general ventricular cavity enlarges is far greater than that assumed by the third ventricle, which always forms but a very small portion of the ventricular space. When the lateral ventricles undergo an increase in size, the enlargement affects all parts more or less equally with the exception of the descending horns referred to above (figs. 1 to 4). But it is to be noted that in the cases examined there is a definite predominance in size of the anterior cornua and adjoining portion of the bodies over the rest of the lateral ventricles. This fact is of importance, in view of the preponderant wasting of cell-bodies in definite regions of the brain mantle in certain cases of atrophy.[1] On comparing the casts it is noted that, as the enlargement increases, the body and anterior and posterior cornua, taken together, form a curve, which is convex upwards (figs. 1 to 4).

Having indicated the general form of the cerebral ventricular space, we now pass to details of structure of this cavity.

The third ventricle, instead of being a narrow plate-like structure, perforated by a centrally placed large aperture representing the middle commissure, m.c., acquires considerable breadth from side to side, while the opening for the middle commissure becomes a narrow canal (figs. 1A, 2A, 3A). Its original shape is somewhat triangular (fig. 1A), presenting an anterior, an upper and a lower border, and two lateral surfaces. Although its shape alters as dilatation occurs, it will nevertheless be convenient to keep to the same division into three borders, noting such modifications as are exhibited.

The third ventricle exhibits on its anterior border, below

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[1] Compare an illustration of nerve-cell degeneration in the frontal cortex, the occipital cortex remaining unaltered, in general paralysis of the insane, given in the Croonian Lectures, 1900, by Dr F. W. Mott, F.R.S., *Brit. Med. Journ.*, 1900, ii. p. 82.

the situation of the foramen of Monro, a deep transverse groove formed by the anterior white commissure, *a.c.* (figs. 1A, 2A, 2B, 3A, 4). Below this is a flattened border, which is sometimes convex, sometimes concave, corresponding to the lamina cinerea, and terminating in a pointed process, directed downwards and forwards, lying in the supra-optic recess, *o.r.* Beneath this is a deep groove formed by the optic commissure, *ch.*, bounded posteriorly by a conical projection, also directed downwards and forwards, representing the interior of the infundibulum.

From this point to the upper opening of the aqueduct of
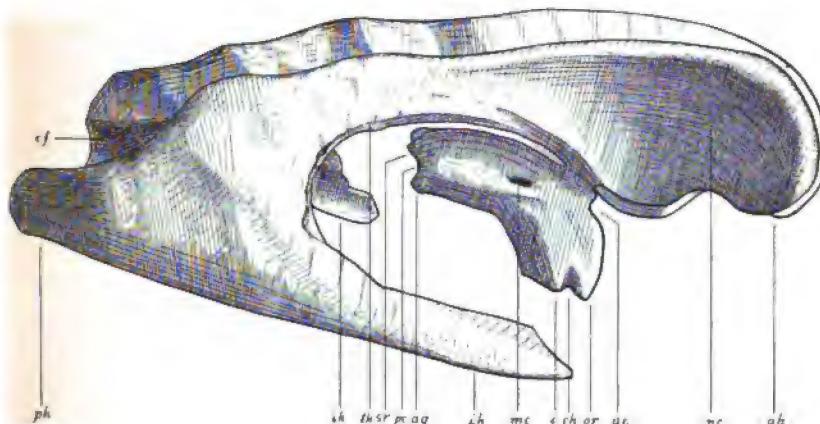
FIG. 2A.

Fig. 2A. Cast of the ventricles of the cerebrum, seen from the right side. Case 2. Male, aged 69 years, suffering from dementia. The ventricular cavity is more dilated than in the preceding case. The lateral ventricles are nearly but not quite symmetrical. The left inferior horn, *i.h.*, is completely and the right partially obliterated by contact of its upper and lower surfaces. The left posterior horn, *p.h.*, is shorter than the right, which is thinner, and curved inwards at its extremity ; each is deeply grooved by the corresponding calcar avis, *c.f.* The supra-pineal recess, *s.r.*, is small.

Observe in this and the succeeding figures the marked enlargement of the lateral ventricles as compared with the third ; the former project much more than the latter into the frontal and occipital lobes, and in addition reach upwards to an unusually high level opposite the vertex. Note also the altered form and direction of the cavity of the third ventricle and the narrowed canal for the middle commissure.

Sylvius, *a.g.*, which is represented by a process directed downwards and backwards, the lower border of the cavity of the third

ventricle forms a concave curve, varying in character in different
cases.   Anteriorly it corresponds to the tuber cinereum and
posterior perforated space, and posteriorly it represents the
upper limit of the tegmentum mesencephali.   The distance
between the anterior end of the inferior border and the upper
opening of the aqueduct of Sylvius increases as the third
ventricular space becomes dilated, and this considerably changes
the form of the anterior inferior end of this cavity, as is shown
in the figures.   Above the upper end of the aqueduct of Sylvius
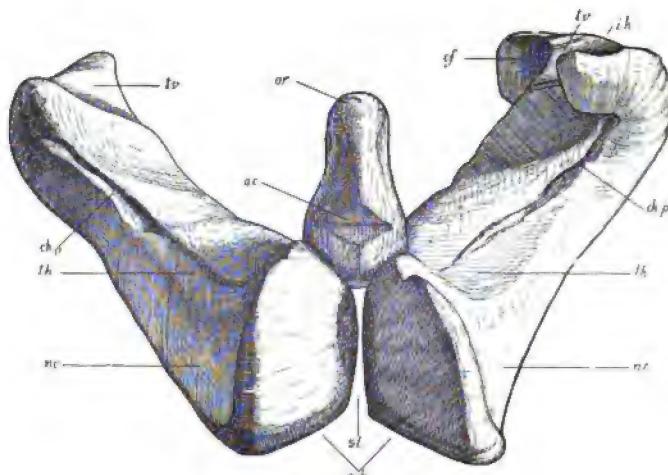
FIG. 2B.

Fig. 2B. The same cast as exhibited in fig. 2A., seen from before.   The massive
      character of the bodies and anterior cornua of the lateral ventricular spaces
      and the increased width of the third ventricular cavity are very striking.
      The surfaces of the lateral ventricles in contact with the caudate nuclei, n.c.,
      and the optic thalami, th., are well seen, as is also the ridge separating
      them, corresponding to the tænia semicircularis.   The surfaces in contact
      with the optic thalami exhibit deep but narrow grooves for the choroid
      plexuses, ch.p.   The trigona ventriculorum, t.v., are also seen.   On the
      anterior aspect of the third ventricle is the deep groove for the anterior com-
      missure, a.c.

is a groove, p.c., corresponding to the posterior white commissure ;
above this again are projections corresponding to the pineal and
supra-pineal recesses, p.r. and s.r., the former being small, and
the latter, which is large (figs. 3A, 3B) and irregular in shape, being
not unfrequently multilocular, and consequently difficult to cast.

That this irregularity in shape is not due to an occasional escape of plaster from the cavity of the third ventricle into the meshes of the pia mater is shown by the fact that this recess can often be seen to be irregularly enlarged and distended with fluid when the brain is placed with its base uppermost, and the cerebellum and pons, together with the mesencephalon, are separated from the splenium of the corpus callosum. This enlargement may be much greater than is shown in the illustrations.

Superiorly, the third ventricle presents a slightly convex border, on which are two parallel grooves (sometimes only one) corresponding to the choroid plexuses of this ventricle. The upper border is slightly convex or nearly straight when only slight dilatation of the cerebral ventricular space is present. When marked dilatation occurs, it becomes much more convex. The third ventricular cavity becomes broad and stumpy at its posterior end, that is, at the junction of superior and inferior borders, when there is marked dilatation.

The outer surfaces of the third ventricle are somewhat irregularly rounded. An antero-posterior ridge, not very sharply defined, is met with immediately below the middle commissure, *m.c.*, dividing each outer surface into an upper portion, sometimes slightly convex, sometimes presenting a shallow groove running from before backwards, and a lower portion convex in outline; the former corresponds to the optic thalamus, the latter to the olfactory field, the internal capsule, and the sub-thalamic tegmentum. Anteriorly are observed the processes connecting the third with the lateral ventricle, *f.m.*; these generally increase in size *pari passu* with that of the lateral ventricles, and are grooved internally and in front for the anterior pillars of the fornix. Between these two processes is a shallow groove, corresponding to the fornix at its junction with the base of the septum lucidum.

The anterior cornua of the lateral ventricles, *a.h.*, diverge from each other as they pass forwards, and have the shape indicated in the figures. They have lost the flattened scale-like character of the undilated cornua, and have become expanded in all directions, passing forwards with an oblique direction, and forming coarse blunt projections. In the situation of the septum lucidum,

s.l., the lateral ventricles approach each other very closely.[1]   None
of these casts, however, show a disappearance of this interval.
It may here be observed that as the size of the ventricles
increases in chronic brain atrophy, the septum lucidum enlarges
in extent and becomes thinned ; occasionally, when the dilatation
of the ventricles is exceedingly large, the nervous material may
here and there be absent, but the ependymal wall still remains,
and is represented by a smooth flattened pyriform surface on the
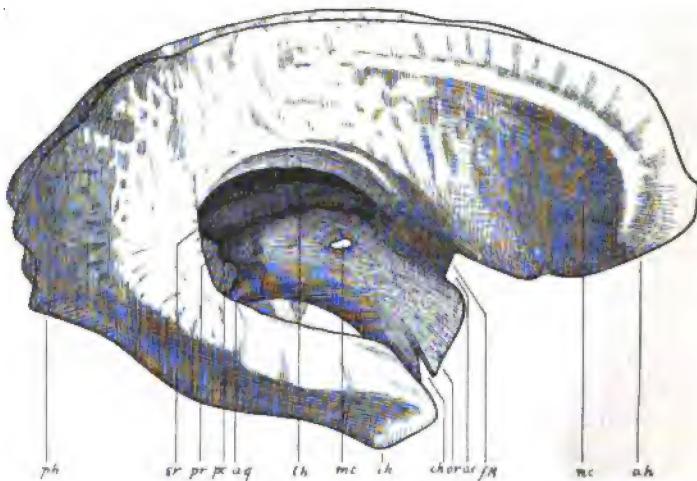

FIG. 3A.

Fig. 3A. Cast of the ventricles of the cerebrum, seen from the right side.   Case
3. Male, aged 51 years, suffering from general paralysis of the insane.   The
ventricular cavity is larger than in the two preceding cases, the chief increase
being in the lateral ventricles.   The form of the third ventricle is similar
to that seen in fig. 2A.   Both inferior cornua are present in the cast, the
right being of large size.

inner side of the cornu (*m.s.*, fig. 4).   Sometimes the cavity of
the septum lucidum becomes filled with plaster, and occasionally
also small collections of plaster, elongated in form and placed
antero-posteriorly, are met with beneath or in the velum inter-
positum, on each side of the upper border of the third ventricle.

[1] In an illustration, after Welcker, in *Quain's Anatomy*, 10th edit., vol.
iii. pt. 1, p. 126, the anterior horns and bodies of the lateral ventricles are
represented too far apart, the interval occupied by the septum lucidum exceeding
a centimetre in transverse measurement.

The upper surface of each anterior cornu is convex, and is continued over the front and lower part of the horn; this surface corresponds to the genu of the corpus callosum, and presents more or less defined grooves radiating from the anterior end of the interval for the septum lucidum, and indicating the forceps minor (figs. 1B, 2B). The outer surface of the anterior cornu presents a large shallow depression, *n.c.*, for the head of the caudate nucleus. It is directed obliquely outwards and downwards; in consequence of this obliquity the anterior cornua are much broader above than below (fig. 2B). The outer border of each anterior cornu becomes very broad and rounded, especially above, as the ventricles become largely dilated;[1] it thus differs very strikingly from the sharp edge which exists in the un-dilated condition.

The body of the lateral ventricle, as it increases in size, becomes thick and broad, so that in section it tends to become elliptical (figs. 1A, 1A with figs. 3A, 3B, 4). On the under surface of the body of the lateral ventricle is seen a flattened elongated depression looking downwards and outwards, *n.c.*, (figs. 1A, 2A, 2B, 3A, 3B), corresponding to the caudate nucleus, and continuous with the large depression on the outer aspect of the anterior horn; while, internal to and slightly below this, is another flattened surface, *th.*, concave from before backwards, corresponding to that portion of the optic thalamus which appears in the lateral ventricle, and presenting a deep antero-posterior groove, *ch.p.*, formed by the choroid plexus of the lateral ventricle, internal to which this surface comes into relation with the lateral band of the fornix. This surface is separated from the groove for the tail of the caudate nucleus by a ridge corresponding to the tænia semicircularis. The upper surface of the body of the lateral ventricle is convex from before backwards, and flattened or slightly convex from side to side. It is marked by transverse grooves, which are apparently caused by an irregular atrophy of the transverse bundles of the corpus callosum. The outer border of the body of the lateral ventricle becomes remarkably thickened and rounded as the dilatation

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[1] The adjoining part of the body is similarly affected. This corresponds to the preponderant wasting of the brain mantle in the region of the frontal and parietal lobes on their outer aspect seen in brain atrophy of the insane.

becomes considerable.   At the outer aspect of the body of the
ventricle, which is at a lower level than the outer border, is a
flattened narrow surface, continuous with the inner surface of
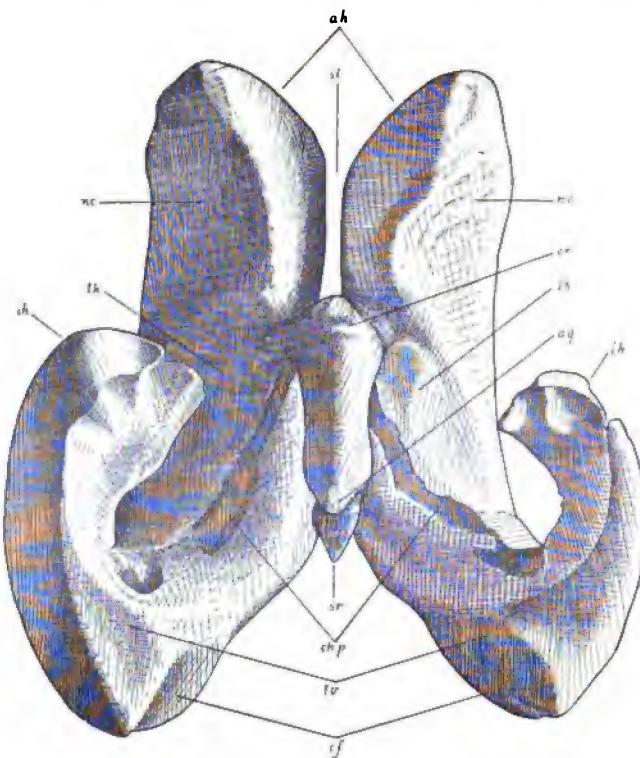
FIG. 3B.

Fig. 3B. The same cast as exhibited in fig. 3A, seen from below.   The right
lateral ventricle is larger than the left.   Both posterior horns, *p.h.*, are
directed backwards, with a very slight inclination outwards on the right
side. · ·On the under surface of the right inferior horn the depression for
the hippocampus major, *h.m.*, is seen, ending anteriorly in the pes.
External to this depression is seen the pes accessorius, ending posteriorly
in the trigonum ventriculi, *t.v.*   The calcar avis, *c.f.*, is large on the right
side, small on the left.   Both posterior cornua are notched.

the anterior cornu, and corresponding to the posterior end of
the dilated septum lucidum (fig. 4).

Posteriorly, the body of the lateral ventricle gives off the
posterior and the inferior cornua.   The shape of the posterior
cornua, which, like anterior, are usually shorter than the inferior,

is variable, and not so readily described in words as represented in a sketch or model. When much dilated, the posterior cornua may be directed inwards posteriorly, so as to be convex outwards (figs. 2A, 2B). The posterior horns, at their junction with the ·
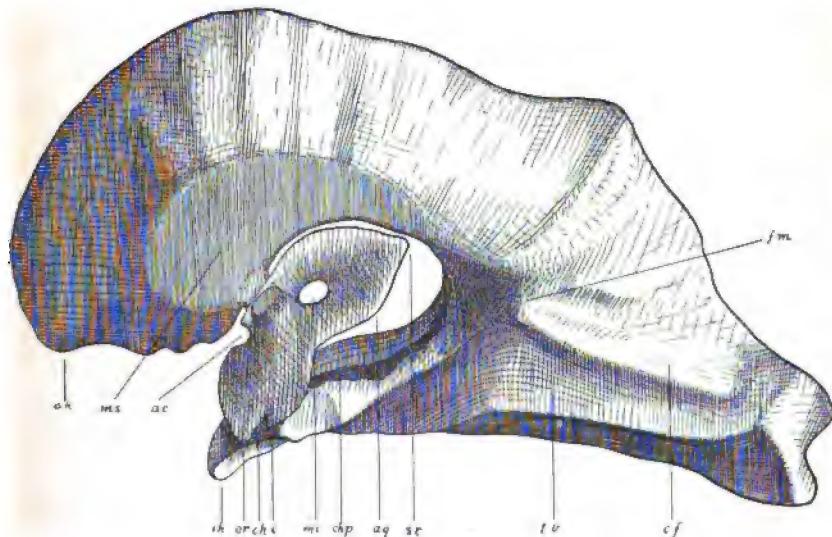
FIG. 4.

Fig. 4. Cast of the third and right lateral ventricles of the cerebrum, seen from the left side. Case 4. Female, aged 55 years, suffering from general paralysis of the insane. The lateral ventricle is the largest of the series. The third ventricle remains relatively small, its form and direction diverging, nevertheless, more from the normal than any of the preceding. The mesial surface of the lateral ventricle, m.s., is seen, corresponding to the septum lucidum, which has undergone an increase in size. The right lateral ventricle (which is larger than its fellow) exhibits towards the root of the posterior cornu a grooved surface, f.m., corresponding to the forceps major of the splenium of the corpus callosum. The posterior cornu, p.h., which curves inwards at its extremity, exhibits a groove corresponding to the calcar avis, c.f., below which is the trigonum. On the upper surface of the inferior horn is a deep groove, ch.p., for the choroid plexus. Below, and in part internal to this, is the groove for the hippocampus major, h.m., external to which is another parallel groove on the under surface of the inferior horn for the pes accessorius or eminentia collateralis.

bodies of the lateral ventricle, present on their inner aspect several deep grooves, separated by well marked ridges (figs. 1A, 3A, 3B), corresponding to the forceps major of the corpus

callosum (*f.m.*, fig. 4). The posterior cornua are sometimes sessile, sometimes prolonged into prominent tips (figs. 2A, 2B, 4); they may be notched posteriorly, the notch corresponding to the groove for the anterior end of the calcarine fissure. On the outer aspect of the posterior cornu, at its junction with the body, one or two large flat grooves are sometimes seen; it is doubtful if these stand in relation to the convolutions on the outer surface of the hemisphere. The upper border of the posterior horn is broad. Below is seen the triangular area corresponding to the trigonum ventriculi, *t.v.* (figs. 2A, 3B, 4). On the anterior aspect of the junction of posterior horn with the body and inferior horn is a surface, flattened from side to side and concave from above downwards, corresponding to the pulvinar of the optic thalamus; this surface is deeply grooved for the choroid plexus.

The inferior cornua, whose general form has been already described, exhibit on the upper surface, close to the inner border, a deep groove, *ch.p.*, formed by the choroid plexus of the lateral ventricle, continuous with that seen on the under surface of the body of this ventricle, and stopping short of the tip of the inferior horn. The under surface of the inferior horn always shows towards its inner border a deep groove, corresponding to the hippocampus major, terminating anteriorly in a well formed foot, representing the cornu ammonis (fig. 3B). The under surface is limited on its outer aspect by a ridge, external to which is a surface, usually narrow, corresponding to the collateral eminence (fig. 4), continuous posteriorly with the triangular depression representing the trigonum ventriculi, *t.v.* The upper surface of the inferior cornu is smooth, and convex from side to side, and also from before backwards; its outer border may be grooved if the dilatation of the ventricles is considerable, and the grooves are in that case traceable to the sulci separating the temporal gyri.

The following table shows in four of the cases examined the capacity of the ventricular cavity of the cerebrum, and its relation to the atrophied brain in each case.

Case.	Mental state.	Age.	Sex.	Capacity of lateral and 3rd ventricles.	Weight of brain.	Brain : ventricles.
1	Dementia,	68	M.	33 c.c.	1165 g.	100 : 2·8
2	,,	69	M.	62 ,,	1230 ,,	100 : 5·0
3	G.P.I.,	51	M.	74 ,,	1380 ,,	100 : 5·4
4	,,	55	F.	157 ,,	1060 ,,	100 : 13·3

The last column was obtained by dividing the weight of the whole brain *plus* that of the brain substance corresponding to the ventricular cavity, by the weight of brain substance corresponding to the ventricular cavity, the latter being obtained by multiplying the capacity of the lateral and third ventricles in cubic centimetres by the specific gravity of the brain (1·038). In Case 1, the brain was not considerably atrophied, nor were the ventricles largely dilated, while in the remaining cases the brain atrophy and ventricular dilatation progressively increased. The actual percentage of brain-wasting is less than that given in the last column, particularly in Case 4, because the original weight of the brain (*i.e.* before wasting commenced) is higher than that taken by an amount of brain substance equal to the amount of fluid in the sub-arachnoid space, the amount of which ·could not be determined.

The general appearance of the lateral ventricles of the cerebrum when dilated shows that the enlargement is due essentially to wasting of white matter. This wasting is exceedingly well seen in the inferior cornua, where, when the wasting is considerable, the bases of several of the temporal sulci (in one case of all) may be represented by grooves on the cast, while the intervening gyri are represented by ridges. On the other hand, the third ventricle, which is bounded by grey matter, is but little ·dilated as compared with the lateral ventricles. The frontal and parietal gyri, however, are not represented on the surface of the casts, the depth of white matter being here considerably thicker than in the temporal lobes. The grooving of the upper surface of the bodies of the lateral ventricles must be attributed to wasting of the nerve bundles of the corpus callosum, and indicates that this structure wastes unequally. The wasting

of the white matter, when marked, is strikingly shown, especially in the temporal lobes, in a series of frontal sections.

The number of cases studied is too small to permit of a comparison of the form of the ventricular cavity in different cases of brain atrophy. It may, however, be observed that in the four cases of senile atrophy (two of which are represented in figs. 1 and 2), the cerebral ventricular cavities, though differing in size from those observed in the two cases of general paralysis (figs. 3 and 4), do not otherwise exhibit any peculiarities of form sufficiently marked to permit any definite distinction to be drawn between the two classes of cases.

In conclusion, the following points relating to the general form of the cerebral ventricular cavity in chronic brain atrophy may be again enumerated. It must be borne in mind that they are not stated as general assertions, applicable to all cases, but merely represent the facts observed in the six cases actually studied.

1. The increase in size of the third ventricle was found to be small as compared with that of the lateral ventricles.

2. The enlargement of the ventricular cavity of the cerebrum is almost wholly due to dilatation of the lateral ventricles, which are everywhere enlarged. The enlargement, however, affects the anterior cornua and bodies more than the rest of the ventricular cavity, while the inferior cornua are often much flattened.

3. The appearance of the ventricular cavity in senile atrophy (four cases) was not observed to differ markedly in its general characters from that present in general paralysis of the insane (two cases).

4. The dilatation is chiefly due to wasting of the white matter of the brain mantle.

TABLE OF REFERENCE LETTERS.

a.c. groove for the anterior white commissure.
a.h. anterior cornu.
aq. upper end of the aqueduct of Sylvius.
c.f. depression for the calcar avis.
ch. groove for the optic chiasma.
ch.p. deep groove for the choroid plexus of the lateral ventricle.
f.m. grooved surface corresponding to the forceps major.

f.M. foramen of Monro.
h.m. depression corresponding to the hippocampus major.
i. the cavity of the infundibulum.
i.h. inferior cornu.
m.c. foramen or canal for the middle grey commissure.
m.s. mesial surface of the lateral ventricle.
n.c. depression for the caudate nucleus.
o.r. optic recess.
p.c. groove for the posterior white commissure.
p.h. posterior cornu.
p.r. pineal recess.
s.l. interval corresponding to the septum lucidum.
s.r. supra-pineal recess.
th. concave surface corresponding to that portion of the optic thalamus which projects into the lateral ventricle.
t.v. trigonum ventriculi.

ON THE ORIGIN OF VERTEBRATES DEDUCED FROM THE STUDY OF AMMOCŒTES. By WALTER H. GASKELL, M.D., LL.D., F.R.S., *University Lecturer on Physiology; Fellow of Trinity Hall.*

PART XI.—THE ORIGIN OF THE VERTEBRATE BODY CAVITY AND EXCRETORY ORGANS; THE MEANING OF THE SOMITES OF THE TRUNK AND OF THE DUCTLESS GLANDS.

IN this series of papers I have considered up to the present the cranial region as a system of segments, and shown how such segments are comparable one by one with the corresponding segments in the prosoma and mesosoma of the presumed arthropod ancestor.

In the spinal region such direct comparison is not possible, as is evident on the face of it; for even among vertebrates themselves the spinal segments are not comparable one by one, so great is the variation, so unsettled is the number of segments in this region. This meristic variation, as Bateson calls it, is the great distinctive character of the spinal region, which distinguishes it from the cranial region with its fixed number of nerves and its substantive rather than meristic variation. At the borderland between the two regions we see how the one type merges into the other; how difficult it is to fix the segmental position of the spino-occipital nerves; how much more variable in number are the segments supplied by the vagus nerves than those anterior to them.

This meristic variation is a sign of instability, of want of fixedness in the type, and is evidence, as already pointed out, that the spinal region is newer than the cranial.

This instability in the number of spinal segments does not necessarily imply a variability in the number of segments of the metasoma of the invertebrate ancestor; it may simply be an expression of adaptability in the vertebrate phylum itself, according to the requirements necessitated by the conversion of a crawling into a swimming animal, and the subsequent conversion of the swimming into a terrestrial or flying animal.

However many may have been the original number of segments belonging to the spinal region, one thing is certain—the segmental character of this region is remarkably clearly shown, not only by the presence of the segmental spinal nerves, but also by the marked segmentation of the mesoblastic structures.

The question therefore that requires elucidation above all others is the origin of the spinal mesoblastic segments, i.e. of the cœlomic cavities of the trunk region, and the structures derived from their walls.

The Origin of the Pronephros, Mesonephros and Body Cavity.

The nature of the primitive trunk segment is conveniently expressed by using v. Wijhe's[1] phraseology. He terms the whole cœlomic cavity the *procœlom*, which is divisible into a ventral unsegmented part, the body cavity or *metacœlom*, and a dorsal segmented part, the somite. This latter part again is divided into a dorsal part, the *epimer*, and a part connecting the dorsal part with the body cavity, to which therefore he gives the name of *mesomer*.

The cavity of the epimer disappears, and its walls form the muscle and cutis plates of the body. The part which forms the muscles is known as the myotome, which separates off from the mesomer, leaving the latter as a blind sac, the *mesocœlom*, communicating by a narrow passage with the body cavity or *metacœlom*. At the same time from the mesomer is formed the sclerotome, which gives rise to the skeletal tissues of the vertebræ, etc., so that v. Wijhe's epimer and mesomer together correspond to the original term protovertebra or somite of Balfour ; and when the myotome and sclerotome have separated off, there is still left the intermediate cell mass of Balfour and Sedgwick, i.e. the sac-like mesocœle of v. Wijhe, the walls of which give origin to the mesonephrotome or mesonephros. Further, according to v. Wijhe, the dorsal part of the unsegmented metacœlom is itself segmented, but not, as in the case of the mesocœle, with respect to both splanchnopleuric and somatopleuric walls. The segmentation is manifest only on the somatopleuric side, and

[1] " Ueber die Mesoderm segmente des Rumpfes u. die Entwick. des Excretion-systems bie Selachiern," von v. Wijhe, *Arch. f. Mikr. Anat.*, Bd. xxxiii. p. 461, 1889.

consists of a distinct series of hollow somatopleuric outgrowths, called by him *hypomeres*, which give rise to the pronephros and the segmental duct.

V. Wijhe considers that the whole metacœlom was originally segmented, because in the lower vertebrates the segmentation reaches further ventralwards, so that in Selachians the body cavity is almost truly segmental. Also in the gill region of Amphioxus the cavities which are homologous with the body cavity arise segmentally.

It is quite unnecessary to trace the history of our knowledge of the development of the excretory vertebrate organs, for it has been admirably done by Rückert[1] up to 1891. I shall therefore refer my reader to that paper, and here only sketch the rise and fall of opinion upon the phylogenetic meaning of such investigations.

As is well known, Balfour and Semper were led, from their embryological researches, to compare the nephric organs of vertebrates with those of annelids, and indeed the nature of the vertebrate segmental excretory organs has always been the fact which has kept alive the belief in the origin of vertebrates from a segmental annelid. These segmental organs thus compared were the mesonephric tubules, and doubts arose, especially in the mind of Gegenbaur, as to the validity of such a comparison, because the mesonephric tubules did not open to the exterior, but into a duct, the segmental duct, which was an unsegmented structure opening into the cloaca; also because the segmental duct, which was the excretory duct of the pronephros, was formed first, and the mesonephric tubules only opened into it after it was fully formed. Further, the pronephros was said to arise from an outbulging of the somatopleuric mesoblast, which extended over a limited number of metameres, and was not segmental, but continuous. Gegenbaur and others therefore argued that the original prevertebrate excretory organ was the pronephros and its duct, not the mesonephros, from which they concluded that the vertebrate must have been derived from an unsegmented type of animal, and not from the segmented annelid type. Such a view, however, has no further reason for

[1] "Entwicklung d. Exkretionsorgane," von J. Rückert, *Anatom. Hefte Merkel, u. Bonnett*, Bd. i., 1891, p. 606.

acceptance, as it was based on wrong premises, for Rückert has shown that the pronephros does arise as a series of segmental nephric tubules, and is not unsegmented; he also has pointed out that in Torpedo the anterior part of the pronephric duct shows indications of being segmented; a statement fully borne out by the researches of Maas[1] on Myxine, who gives the clearest evidence that in this animal the anterior part of the pronephric duct is formed by the fusion of a series of separate ducts, each of which in all probability once opened out separately to the exterior.

Rückert therefore concludes that Balfour and Semper were right in deriving the segmental organs of vertebrates from those of annelids, but that the annelid organs are represented in the vertebrate, not by the mesonephric tubules, but by the pronephric tubules and their ducts, which originally opened separately to the exterior. By the fusion of such tubules the anterior part of the segmental duct was formed, while its posterior part was brought about either by a later cœnogenetic lengthening, or is the only remnant of a series of pronephric tubules which originally extended the whole length of the body, as suggested also by Maas and Boveri. Rückert therefore supposed that the mesonephric tubules were a secondary set of nephric organs, which were not necessarily directly derived from the annelid nephric organs.

V. Wijhe, in his original paper,[2] did not consider that it was possible to derive any of the vertebrate excretory organs from an invertebrate type, because they were not represented in Amphioxus, and therefore arose after the chordate type of animal had arisen; in any case, he agreed with Rückert that the mesonephric tubules were not homologous with the nephric tubules of the annelid, and did not think that Rückert's suggestion that the pronephros is homologous with the annelid nephric organs was likely to find general acceptance until the differences between annelids and vertebrates in other respects— such as the central nervous system of the former with its œsophageal ring—are satisfactorily explained.

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[1] "Ueber Entwick. stadien d. Vorniere u. Urniere bei Myxine," von O. Maas, *Zool. Jahrbuch*, Bd. x., 1897, p. 473.

[2] *Op. cit.*, p. 511.

The discovery of the nephric tubules of Amphioxus by Boveri[1] and Weiss[2] has removed v. Wijhe's difficulty, and has still further confirmed Rückert's suggestion, for Boveri looks upon these organs as pronephric although they are confined to the branchial region, and considers that the pronephric organs originally extended along the whole trunk region, because he considers that the branchiæ also extended along the whole length of the body.

With respect to his further remark about the need of a satisfactory explanation of the differences between the annelid and vertebrate nervous systems, before Rückert's suggestion is likely to find general acceptance, I venture to hope that the explanation I have given in this series of papers will prove satisfactory to him.

At present, then, Rückert's view is the most generally accepted one:—that the original annelid nephric organs are represented by the pronephric tubules and the pronephric duct, not by the mesonephric tubules, which are a later formation.

This latter statement would hold good if the mesonephric tubules were found entirely in segments posterior to those containing the pronephric tubules; such, however, is said not to be the case, for the two sets of organs are said to overlap in some cases; even when they exist in the same segments the former are said always to be formed from a more dorsal part of the cœlom than the pronephros, always to be a later formation, and never to give any indication of communicating with the exterior except by way of the pronephric duct.

The recent observations of Brauer[3] on the excretory organs of the Gymnophiona throw great doubt on the existence of mesonephric and pronephric tubules in the same segment. He criticises the observations on which such statements are based, and concludes that, as in *Hypogeophis*, the nephrotome which is cut off after the separation of the sclero-myotome gives

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[1] "Die Nieren Canälchen des Amphioxus," von Th. Boveri, *Zool. Jahrbuch*, Bd. v., 1892, p. 429.

[2] "Excretory tubules in *Amphioxus lanceolatus*," by F. E. Weiss, *Q. J. Micr. Sci.*, vol. xxxi., 1890.

[3] "Beiträg. z. Kenntniss d. Entwick. u. Anat. d. Gymnophionen."—III. "Die Entwicklung d. Excretionsorgane," von A. Brauer, *Zool. Jahrbuch*, Bd. 16, p. 1, 1902.

origin to the pronephros in the more anterior regions, just as it gives origin to the mesonephros in the more posterior regions.

In fact, the observations of v. Wijhe and others do not in reality show that two excretory organs may be formed in one segment, the one mesonephric from the remains of the mesomer and the other pronephric from the hypomer, but rather that in such cases there is only one organ,—the pronephros,—part of which is formed from the mesomer and part from the hypomer. Brauer goes further than this, and doubts the validity of any distinction between pronephros and mesonephros, on the ground of the former arising from a more ventral part of the procœlom than the latter; for, as he says, it is only possible to speak of one part of the somite as being more ventral than another part when both parts are in the same segment; so that if pronephric and mesonephric organs are never in the same segment, we cannot tell with certainty that the former arises more ventrally than the latter.

These observations of Brauer strongly confirm Sedgwick's original statement that the pronephric and mesonephric organs are homodynamous organs, in that they are both derived from the original serially situated nephric organs, the differences between them being of a subordinate nature, and not sufficient to force us to believe that the mesonephros is an organ of quite different origin to the pronephros.

So also Price,[1] from his investigations of the excretory organs of Bdellostoma, considers that in this animal both pronephros and mesonephros are derived from a common embryonic kidney, to which he gives the name 'holonephros.'

Brauer also is among those who conclude that the vertebrate excretory organs were derived from those of annelids; he thinks that the original ancestor possessed a series of similar organs over the whole pronephric and mesonephric regions, and that the anterior pronephric organs, which alone form the segmental duct, became modified for a larval existence,—that their peculiarities were adaptive rather than ancestral.

This view seems to me very far-fetched, without any sufficient grounds for it; according to the much more probable and

[1] "Development of the excretory organs of *Bdellostoma Stouti*," by G. C. Price, *Zool. Jahrbuch*, vol. x. p. 205, 1897.

reasonable view, the pronephros represents the oldest and original excretory organs, while the mesonephros are later formations. Brauer's evidence seems to me to signify that the pronephros, mesonephros and metanephros are all serially homologous, and the pronephros bears much the same relation to the mesonephros that the mesonephros does to the metanephros. The great distinction of the pronephros is that it, and it alone, forms the segmental duct.

We may sum up the conclusions as follows:—

1. The pronephric tubules and the pronephric duct are the oldest part of the excretory system, and are distinctly in evidence for a few segments only in the most anterior part of the trunk region immediately following the branchial region. They differ also from the mesonephric tubules by not being so clearly segmental with the myotomes.

2. The mesonephric tubules belong to segments posterior to those of the pronephros, are strictly segmental with the myotomes, and open into the pronephric duct.

3. All observers are agreed that the two sets of excretory organs resemble each other in very many respects, as, though they arose from the same series of primitive organs, and according to Sedgwick and Brauer, no distinction of any importance does exist between the two sets of organs. Other observers, however, consider that the pronephric organs, in part at all events, arise from a part of the nephroccele more ventral than that which gives origin to the mesonephric organs, and that this difference in position of origin, combined with the formation of the segmental duct, does constitute a true morphological distinction between the two sets of organs.

4. All the recent observers are in agreement that the vertebrate excretory organs strongly indicate a derivation from the segmental organs of annelids.

The very strongest support has been given to this last conclusion by the recent discoveries of Boveri[1] and Goodrich[2] upon the excretory organs of Amphioxus. According to Boveri, the nephric tubules of Amphioxus open into the dorsal coelom by

[1] *Op. cit.*

[2] "On the structure of the excretory organs of Amphioxus," by E. S. Goodrich, *Q. J. Micr. Sci.*, vol. 45, p. 493, 1902.

one or more funnels. Around each funnel are situated groups of peculiar cells, called by him 'Fadenzellen,' each of which sends a long process across the opening of the funnel. Goodrich has examined these Fadenzellen and found that they are typical pipe cells or solenocytes, such as he has described[1] in the nephridial organs of various Polychætes. Also, just as in the Polychætes, the ciliated nephric tubule has no internal funnel-shaped opening into the cœlom, but terminates in these groups of solenocytes. "Each solenocyte[2] consists of a cell body and nucleus situated at the distal free extremity of a delicate tube; the proximal end of the tube pierces the wall of the nephridial canal and opens into its lumen. A single long flagellum arising from the cells works in the tube and projects into the canal."

The exceedingly close resemblance between the organs of Amphioxus and those of Phyllodoce, as given in his paper, is most striking, and, as he says, forces the conclusion that the excretory organs of Amphioxus are essentially identical with the nephridia of certain polychæte worms.

It is to me most interesting to find that the very group of annelids, the Polychæta, which possess solenocytes so remarkably resembling those of the excretory organs of Amphioxus, are the highest and most developed of all the Annelida. My contention has been throughout, that the Protostraca, from which the three groups of Crustacea, Arachnida and Vertebrata are supposed to have arisen, must have been closely allied to the highest group of annelids, the Chætopoda, and not to any lower group; the evidence of Amphioxus suggests strongly that the protostracan ancestor of the vertebrates arose from the highest group of the Chætopods, viz., the Polychæta.

The evidence which I have given in my former papers of this series points, however, strongly to the conclusion that the vertebrate did not arise from members of the Protostraca near to the polychæte stock but rather from members in which the arthropod characters had already become well developed; members, therefore, which were nearer the Trilobites than the

[1] "On the nephridia of the Polychæta," parts i., ii., iii., *Q. J. Micr. Sci.*, vols. 40, 41, 43.

[2] "On the excretory organs of Amphioxus," by E. S. Goodrich, *Proc. Roy. Soc.*, vol. lxix. p. 351, 1902.

Polychætes. Such early arthropods would very probably have
retained in part excretory organs of the same character as those
found in the original polychæte stock, and thus account for the
presence of solenocytes in the excretory organs of Amphioxus.

In connection with such a possibility I should like to draw
attention to the observations of Claus [1] and Spangenberg [2] on the
excretory organs of Branchipus—that primitive phyllopod, which
is recognised as the nearest approach to the trilobites at present
living.

According to Claus, an excretory apparatus exists in the
neighbourhood of each ganglion, and Spangenberg finds a perfectly
similar organ in the basal segment of each appendage; a system,
therefore, of excretory organs as segmentally arranged as those of
Peripatus. Claus considered that although these organs formed
an excretory system, it was not possible to compare them with
the annelid segmental organs, because he thought the cells in
question arose from ectoderm.

Now, the striking point in the description of the excretory
cells in these organs, as described both by Claus and Spangenberg, [3]
is that they closely resemble the pipe cells or solenocytes of
Goodrich; each cell possessed a long tube-like projection, which
opens on the surface. They appear distinctly to belong to the
category of flame cells, and resemble solenocytes more than any-
thing else.

According to Goodrich, the solenocyte is probably an ecto-
dermal cell, so that even if it prove to be the case, as Claus
thought, that these pipe cells of Branchipus are ectodermal,
they would still claim to be derived from the segmental
organs of annelids, especially of the Polychæta, being, to use
Goodrich's nomenclature, true nephridial organs, as opposed
to cœlomostomes.

I cannot find in the later literature of the subject any in-
vestigations on these excretory organs; in view of the great
importance of this question, I venture to hope that the discoverer
of the solenocyte will, in the course of his further researches,

[1] " Untersuch. üb. d. Organism. u. Entwick. v. Branchipus u. Artemia,"
von Claus, *Arbeit. a. d. Zool. Instit.*, Wien, Bd. 6, p. 267, 1886.

[2] Spangenberg, *Zeitschr. f. wissent. Zool.*, Bd. 25, 2, 1875.

[3] Cf. *op. cit.*, fig. 6, taf. 1.

take into consideration these organs of Branchipus, and let us know whether they are of the nature of solenocytes or not.

These observations of Claus and Spangenberg suggest not only that the primitive arthropod of the trilobite type possessed segmental organs in every segment directly derived from those of a polychæte ancestor, but also that such organs were partly somatic and partly appendicular in position. Such a suggestion is in strict accord with the observations of Sedgwick[1] on the excretory organs of the most primitive arthropod known, viz., Peripatus, where also the excretory organs which are true segmental organs are partly somatic and partly appendicular. Further, the excretory organs of the Scorpion and Limulus group are again partly somatic and partly appendicular, receiving the name of coxal glands because there is a ventral projection of the gland into the coxa of the corresponding appendage.

Judging from all the evidence available, it is probable that when the arthropod stock arose from the annelids, simultaneously with the formation of appendages, the segmental somatic nephric organs of the latter extended ventrally into the appendage, and thus formed a segmental set of excretory organs, which were partly somatic partly appendicular in position, and might therefore be called coxal glands.

Further, the evidence of Miss Sheldon[2] in Peripatus shows that such a diverticulum of the original nephrocœle into the appendage, as would naturally be expected, is formed from the somatopleuric layer alone, just as has been stated to be the case in the formation of at all events a portion of the pronephric organ in the vertebrate.

As already stated, all investigators of the origin of the vertebrate excretory organs are unanimous in considering them to be derived from segmental organs of the annelid type. I naturally agree with them, but, in accordance with my theory, would substitute the words ' primitive arthropod ' for the word ' annelid,' for all the evidence I have accumulated in the preceding papers of this series points directly to that conclusion. Further, the most

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[1] " A monograph of the development of *Peripatus Capensis*," by A. Sedgwick, *Studies from the Morphol. Lab.*, *Cambridge*, vol. iv. pt. 1, 1888.

[2] " On the development of *Peripatus Nova-Zealandiæ*," by L. Sheldon, *Studies from the Morphol. Lab.*, *Cambridge*, vol. iv. pt. 3, 1889, pl. xxvi. fig. 21*b*.

primitive of the three sets of vertebrate segmental organs—the pronephros, mesonephros and metanephros—is undoubtedly the pronephros; consequently the pronephric tubules are those which I consider to be more directly derived from the coxal glands of the primitive arthropod ancestor. Such a derivation appears to me to afford an explanation of the difficulties connected with the origin of the pronephros and mesonephros respectively, which is more satisfactory than that given by the direct derivation from the annelid.

The only living animal which we know of as at all approaching the most primitive arthropod type is, as pointed out by Korschelt and Heider, Peripatus; and Peripatus, as is well known, possesses a true cœlom and true cœlomic excretory organs in all the segments of the body.

Sedgwick shows that at first a true cœlom, as good as that of the annelids, is formed in each segment of the body, and that then this cœlom (which represents in the vertebrate v. Wijhe's procœlom) splits into a dorsal and a ventral part. In the anterior segments of the body the dorsal part disappears (presumably its walls give origin to the mesoblast from which the dorsal body muscles arise), while the ventral part remains and forms a nephrocœle, giving origin to the excretory organs of the adult.

According to v. Kennel, the cavity becomes divided into three spaces, which for a time are in communication—a lateral (I.), a median (II.), and a dorso-median (III.). The dorso-median portion becomes partitioned off, and this, as well as the greater part of the lateral portion, which lies principally in the foot, is used up in providing elements for the formation of the body and appendage muscles respectively and the connective tissue.

In fig. 1, I reproduce v. Kennel's diagram of a section across a Peripatus embryo, in which I. represents the lateral appendicular part of the cœlom, II. the ventral somatic part, and III. the dorsal part which separates from the ventral and lateral parts, and, as its walls give origin largely to the body muscles, may be called the myocœle. The muscles of the appendages are formed from the ventral part of the original procœlom, just as I have argued is the case with the muscles of the splanchnic segmentation in vertebrates. Sedgwick states that the ventral part of the cœlom extends into the base of each appendage, and there

forms the end sac of each nephric tubule, into which the nephric funnel opens, thus forming a coxal gland; this end sac or vesicle in the appendage is called by him the internal vesicle (*i.v.*), because later another vesicle is formed from the ventral cœlom in the body itself, close against the nerve cord on each side, which he calls the external vesicle (*e.v.*). (*Cf.* fig. 2, taken from Sedgwick.) This second vesicle is, according to him,
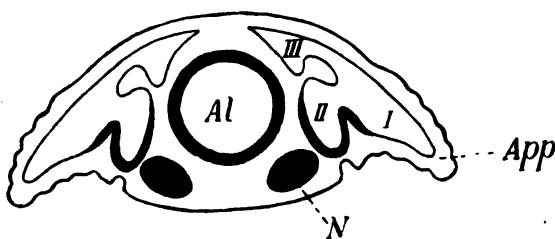
FIG. 1.—Transverse section of Peripatus embryo (after v. Kennel). *Al.*, alimentary canal; *N.*, nerve cord; *App.*, appendage; *I, II, III*, the three divisions (lateral, median, and dorso-median) of the cœlom.
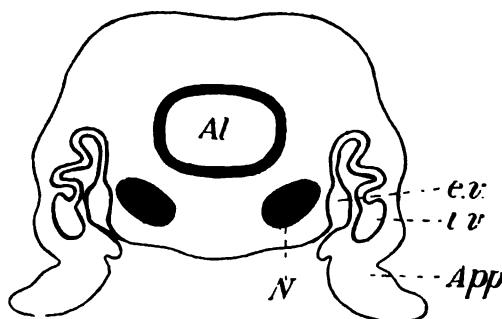
FIG. 2.—Section of Peripatus (after Sedgwick). *Al.*, alimentary canal; *N.*, nerve cord; *App.*, appendage; *i.v.*, internal, and *e.v.*, external vesicles of the segmented excretory tubule (coxal gland).

formed later in the development from the nephric tubule of the internal vesicle, so that it discharges its contents to the exterior by the same opening as the original tubule. Of course, as he points out, the whole system of internal and external vesicles and nephric tubules are all simply derivatives of the original ventral part of the cœlom or nephrocœle.

Here, then, in Peripatus, and presumably therefore in members

of the Protostraca, we see that the original segmental organs of the annelid have become a series of nephric organs, which extended into the base of the appendages, and may therefore be called coxal glands; also it is clear from Sedgwick's description that if the appendages disappeared, the nephric organs would still remain, not as coxal glands, but as purely somatic excretory glands. They would still be homologous with the annelid segmental organs or with the coxal glands, but would arise *in toto* from a part of the ventral cœlom or nephrocœle more dorsal than the former appendicular part, because the appendages and their enclosed cœlom are always situated ventrally to the body. Again, according to Sedgwick, the nephric tubules are connected with two cœlomic vesicles, the one in the appendage, the internal vesicle, and the other, the so-called bladder, or the external vesicle in the body itself, close against the nerve cord. Sedgwick appears to consider that either of these vesicles may form the end sac of a nephric tubule, for he discusses[1] the question whether the single vesicle which in each case gives origin to the nephridia of the first three legs corresponds to the internal or external vesicle. He decides, it is true, in favour of the internal vesicle, and therefore considers the excretory organ to be appendicular, *i.e.* a coxal gland, in these segments as well as in those more posterior; still ,the very discussion shows that in his opinion at all events the external vesicle might represent the end sac of the tubule, in the absence of the internal or appendicular vesicle.

Such an arrangement as Sedgwick describes in Peripatus is the very condition required to give rise to the pronephric and mesonephric tubules, as deduced by me from the consideration of the vertebrate, and harmonises and clears up the controversy about the mesonephros and pronephros in the most satisfactory manner.

Both pronephros and mesonephros are seen to be derivatives of the original annelid segmental organs, not directly from an annelid, but by way of an arthropodan ancestor; the difference between the two being simply that the pronephric organs were coxal glands, and indicate therefore the presence of the original metasomatic appendages, while the mesonephric organs were

[1] *Op. cit.,* p. 140.

homologous organs, formed in segments of later origin which had lost their appendages.

For this reason the pronephros is said to be formed, in part at least, from a portion of the cœlom situated more ventrally than the purely somatic part which gives rise to the mesonephros. For this reason Sedgwick, Brauer, etc. can say that the meso-nephros is strictly homodynamous with the pronephros; while equally Rückert, Semon and v. Wijhe can say it is not homo-dynamous, in so far that the two organs are not derived strictly from absolutely homologous parts of the cœlom.

For this reason Semon can speak of the mesonephros as a dorsal derivative of the pronephros, just as Sedgwick says that the external or somatic vesicle of Peripatus is a derivative of the appendicular nephric organ. For this reason the pronephros, or rather a part of it, is always derived from the somatopleuric layer, for, as is clear from Miss Sheldon's drawing,[1] the part of the cœlom in Peripatus which dips into the appendage is derived from the somatopleuric layer alone.

Such a cœlom as that of Peripatus, fig. 1, would represent the origin of the vertebrate cœlom, and would therefore represent the procœlom of v. Wijhe; and in accordance we see that it separates into a dorsal part, the walls of which give origin to the somatic muscles, or at all events to the great longitudinal dorsal muscles of the animal, and a ventral part, which forms a nephrocœle, dips into the appendage, and gives origin to the muscles of the appendage. In the vertebrate, after the somatic dorsal part or myocœle has separated off, there is left a ventral part, which forms a nephrocœle in the trunk region, and gives origin to the splanchnic striated muscles in the cranial region, *i.e.* to the muscles which, according to my theory, were once appendicular muscles. This ventral nephrocœlic part is divisible in the trunk into a segmented part, which forms the excretory organs proper, and an unsegmented part, the metacœle or true body cavity of the vertebrate.

This comparison of the procœlom of the vertebrate and arthropod signifies that the vertebrate metacœle was directly derived by ventral downgrowth from the arthropod nephrocœle, so that if, as I suppose, the vertebrate nervous system represents

[1] *Loc cit.*

the conjoined nervous system and alimentary canal of the
arthropod, then the vertebrate metacœle, or body cavity, must
have been originally confined to the region on each side of the
central nervous system, and from this position have spread
ventrally to ultimately enclose the new formed vertebrate gut.
This means that the body cavity (metacœle) of the vertebrate is
not the same as the body cavity of the annelid, but corresponds
to a ventral extension of the nephrocœle, or ventral part of
such body cavity.

Such a phylogenetic history is most probable, because it
explains most naturally and simply the facts of the development
of the vertebrate body cavity; for the mesoblast always
originates in the neighbourhood of the notochord and central
nervous system, and the lumen of the body cavity always
appears first in that region, and then extends laterally and
ventrally on each side until it reaches the most ventral surface of
the embryo, thus forming a ventral mesentery, which ultimately
disappears, and the body cavity surrounds the gut, except for
the dorsal mesentery. Thus Shipley [1] in his description of the
formation of the mesoblastic plates which line the body cavity
in Ammocœtes describes them as commencing in two bands
of mesoblast situated on each side, close against the commencing
nervous system : " these two bands [2] are separated dorsally by
the juxtaposition of the dorsal wall of the mesenteron and the
epiblast, and ventrally by the hypoblastic yolk-cells which are
in contact with the epiblast over two-thirds of the embryo.
Subsequently, but at a much later date, the mesoblast is
completed ventrally by the downgrowth on each side of these
mesoblastic plates. The subsequent downward growth is
brought about by the cells proliferating along the free ventral
edge of the mesoblast; these cells then growing ventralwards,
pushing their way between the yolk-cells and epiblast."

The derivation of the vertebrate pronephric . segmental
organs from the metasomatic coxal glands of a primitive
arthropod would mean, if the segmental organs of Peripatus be
taken as the type, that such glands opened to the exterior on

[1] "On some points in the development of *Petromyzon fluviatilis*," by A. E.
Shipley, *Q. J. Micr. Sci.*, 1887.
[2] *Op. cit.*, pp. 5 and 6, fig. 16.

every segment, either at the base of the appendage or on the appendage itself.

It is taken for granted by most observers that the pronephric segmental organs once opened to the exterior on each segment, and then, from some cause or other, ceased to do so, and the separate ducts, by a process of fusion, came to form a single segmental duct, which opened into the cloaca. Many observers have been led to the conclusion that the pronephric duct is epiblastic in origin, although, from its position in the adult, it appears far removed from all epiblastic formations. However, at no time in the developmental history is there any clear evidence of actual fusion of any part of the pronephric organ with the epidermis, and the latest observer, Brauer, is strongly of opinion that there is never sufficiently close contact with the epidermis to warrant the statement that the epiblastic cells take part in the formation of the duct. All that can be said is, that the formation of the duct takes place at a time when the pronephric diverticulum is in close propinquity to the epidermis, before the ventral downgrowth of the myotome has taken place.

The formation of the anterior portion of the pronephric duct is, according to Maas[1] in Myxine, and Wheeler[2] in Petromyzon, undoubtedly formed by the fusion of a number of pronephric tubules, which, according to Maas, are clearly seen in the youngest specimens as separate segmental tubes; each of these tubules is supplied by a capillary network from a segmental branch of the aorta, as in the tubules of Amphioxus according to Boveri, and does not possess a glomerulus.

The posterior part of the duct into which the mesonephric tubules enter possesses also a capillary network, which Maas considers to represent the original capillary network of a series of pronephric tubules, the only remnant of which is the duct into which the mesonephric tubule opens. He therefore argues that the pronephric duct indicates a series of pronephric tubules, which originally extended along the whole length of the body,

[1] *Op. cit.*

[2] " Development of the urinogenital organs of the Lamprey," by Wheeler, *Zool. Jahrbuch*, Bd. xiii. p. 1, 1899.

and were supplanted by the mesonephric tubules, which also belonged to the same segments.

I also think that the paired appendages, which have left as signs of their past existence the pronephric tubules, originally in the invertebrate stage existed on every segment of the body, but I do not consider that such a statement is at all equivalent to saying that such pairs of tubules must have existed upon every one of the segments existing at the present day; for it seems to me that Rückert is much more likely to be right when he says that in Selachians the duct clearly does grow back, and is not formed throughout *in situ*; so that he gives a double explanation of the formation of the duct: a palingenetic anterior part formed by the fusion of the extremities of the original excretory tubules, to which a posterior cœnogenetic lengthening has been added.

It does not seem to me at all necessary that the immediate invertebrate ancestor of the vertebrate should have possessed excretory organs which opened out separately to the exterior on each segment; already, in the invertebrate stage, a fusion may have taken place, and so a single duct have been acquired for a number of organs. Such a suggestion has been made by Rückert,[1] because of the fact discovered by Cunningham and E. Meyer that the segmental organs of *Lanice conchilega* are on each side connected together by a single strong longitudinal canal. I would, however, go further than this, and say that, even although the nephric organs of the polychæte ancestor opened out on every segment, and although the primitive arthropodan ancestor derived from such polychæte possessed coxal glands which opened out either on or at the base of each appendage, similarly to those of Peripatus, yet the immediate arthropodan ancestor, with its palæostracan affinities, may have already possessed metasomatic coxal glands, all of which opened into a single duct, with a single opening to the exterior.

Judging from Limulus, such was very probably the case, for Patten[2] and Hazen have shown (1) that the coxal glands of Limulus are segmental organs belonging to the prosomatic

[1] "Ueber die Entstehung der Excretionsorgane bei Selachiern," von J. Rückert, *Archiv f. Anatomie*, 1888, p. 258.

[2] "The development of the coxal gland, etc. of *Limulus polyphemus*," *Journ. of Morph.*, vol. xvi. p. 459, 1900.

segments, (2) that the organs belonging to the cheliceral and ectognathic segments are not developed, (3) that the four glands belonging to the endognaths become connected together by a stolon, which communicates with a single nephric duct, opening to the exterior on the basal segment of the 5th prosomatic appendage (the last endognath). At no time is there any evidence of any separate openings or any fusion with the ectoderm such as might indicate separate openings of these prosomatic coxal segmental organs.

Thus we see that in Limulus, which is presumably much nearer the annelid condition than the vertebrate, all evidence of separate nephric ducts opening to the exterior on each prosomatic segment has entirely disappeared, just as is the case in the metasomatic coxal glands (*i.e.* the pronephros) of the vertebrate. What is seen in the prosomatic region of Limulus, and doubtless also of the Eurypterids, may very probably have occurred in the metasomatic region of the immediate invertebrate ancestors of the vertebrate, and so account for the single pronephric duct belonging to a number of pronephric organs.

The interpretation of these various embryological investigations may be summed up as follows :—

1. The ancestor of the vertebrates possessed a pair of appendages on each segment; into the base of each of these appendages the segmental excretory organ sent a diverticulum, thus forming a coxal gland.

2. Such coxal glands, even in the invertebrate stage, may have discharged into a common duct which opened to the exterior most posteriorly.

3. Then, from some cause, the appendages were rendered useless and dwindled away, leaving only the pronephric organs to indicate their former presence. At the end of this stage the animal possessed vertebrate characteristics.

4. For the purpose of increasing mobility, of forming an efficient swimming instead of a crawling animal, the body segments increased in number, always, as is invariably the case, by the formation of new ones between those already formed and the cloacal region, and so of necessity caused an elongation of the pronephric duct; into this there opened now the ducts of the segmental organs formed by recapitulation, those there-

fore belonging to the body segments—mesonephric—having
nothing to do with appendages, for these latter had already
ceased to exist functionally, and would not therefore be repeated
with each meristic repetition.

This, so to speak, passive lengthening of the pronephric duct
in consequence of the lengthening of the early vertebrate body
by the addition of metameres, each of which contained only
mesonephric and no pronephric tubules, is to my mind an
example of a principle which has played an important part in
the formation of the vertebrate, viz., that the meristic variation
by which the spinal region of even the lowest of existing verte-
brates has been formed has largely taken place in the vertebrate
phylum itself, and that such changes must be eliminated before
we can picture to ourselves the prevertebrate condition. As an
example, I may mention the remarkable repetition of similar
segments pictured by Bashford Dean [1] in Bdellostoma. Such
repetition leads to passive lengthening of such parts as are
already formed but are not meristically repeated : such are
the notochord, the vertebrate intestine, the canal of the
spinal cord, and possibly the lateral line nerve. The fuller
discussion of this point means the discussion of the formation
of the vertebrate alimentary canal; I will therefore leave it
until I come to that part of my subject, and only say here that
the evidence seems to me to point to the conclusion that at the
time when the vertebrate was formed, the respiratory and cloacal
regions were very near together, the whole of the metasoma being
represented by the region of the pronephros alone.

Here, as always, the evidence of Ammocœtes tends to give
definiteness to our conceptions, for Wheeler [2] points out that up
to a length of 7 mm. the pronephros only is formed; there is no
sign of the more posteriorly formed mesonephros. Now we
know, as pointed out in Part VIII. of this series,[3] this is the time
of Kupffer's larval stage of Ammocœtes. This is the time during
which the invertebrate stage is indicated in the ontogeny, so
that, in accordance with all that has gone before, this means

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[1] "On the embryology of *Bdellostoma Stouti*," by Bashford Dean, *Festschr.
z. siebenzigsten Geburtstag v. C. v. Kupffer*, Jena, 1899.

[2] *Op. cit.*

[3] *This Journ.*, vol. xxxiv. p. 577.

that the metasoma of the invertebrate ancestor was confined to the region of the pronephros.

Again, take Shipley's account of the development of Petromyzon.[1] He says:

" The alimentary canal behind the branchial region may be divided into three sections. Langerhans has termed these the stomach, midgut and hindgut, but as the most anterior of these is the narrowest part of the whole intestine, it would perhaps be better to call it œsophagus. This part of the alimentary canal lies entirely in front of the yolk, and is, with the anterior region which subsequently bears the gills, raised from the rest of the egg when the head is folded off. It is supported by a dorsal mesentery, on each side of which lies the head kidney (pronephros)." Further on he says:[2]

" The hindgut is smaller than the midgut; its anterior limit is marked by the termination of the spiral valve, which does not extend into this region. The two segmental ducts open into it just where it turns ventrally to open to the exterior by a median ventral anus. Its lumen is from an early stage lined with cells which have lost their yolk, and it is in wide communication with the exterior from the first. This condition seems to be, as Scott suggests, connected with the openings of the ducts of the pronephros, for this gland is completed and seems capable of functioning long before any food could find its way through the midgut, or indeed before the stomodæum has opened."

Is there no significance in this statement of Shipley? Even if it be possible to find some special reason why the branchial and cloacal parts of the gut are freed from yolk and lined with serviceable epithelium a long time before the midgut, why should a bit of the midgut, which Shipley calls the œsophagus, which is connected with the region of the pronephros, and not of the branchiæ, differ so markedly from the rest of the midgut? Surely the reason is that the branchial region of the gut, the pronephric region of the gut, and the cloacal region of the gut belong to a different and earlier phase in the phylogenetic history of the Ammocœtes than the midgut between the pronephric and cloacal regions. This observation of Shipley fits in with and emphasises the view that the original animal from

[1] *Op. cit.,* p. 26.   [2] *Op. cit.,* p. 28.

which the vertebrate arose consisted of a cephalic and branchial region, followed by a pronephric and cloacal region; the whole intermediate part of the gut, which forms the midgut, with its large lumen and spiral valve, and which belongs to the meso-nephric region, being a later formation brought about by the necessity of increasing the length of the body.

The Origin of the Somatic Trunk Musculature and the Formation of an Atrial Cavity.

Next comes the question, why was the pronephros not repeated in the meristic repetition that took place during the early vertebrate stage? what, in fact, caused the disappearance of the metasomatic appendages, and the formation of the smooth body surface of the fish?

The embryological evidence given by v. Wijhe and others of the manner in which the original superficially situated pronephros is removed from the surface and caused to assume the deeper position, as seen in the later embryo, is perfectly clear and uniform in all the vertebrate groups. The diagrams at the end of v. Wijhe's paper, which I reproduce here, illustrate the process which takes place. At first the myotome (A, fig. 3) is confined to the dorsal region on each side of the spinal cord and noto-chord. Then it (B, fig. 3) separates from the rest of the somite and commences to extend ventrally, thus covering over the pronephros and its duct, until finally (C, fig. 3) it reaches the mid-ventral line on each side, and the foundations of the great somatic body muscles are finally laid.

In order, therefore, to understand how the obliteration of the appendages took place, we must first find out what is the past history of the myotomes; why are they confined at first to the dorsal region of the body, and afterwards extend to the ventral region, forcing by their growth an organ that was originally external in situation to become internal?

In the original discussion at Cambridge, I was accused of violating Principle 5,[1]—In phylogeny we must look at the most elementary of the animals whose ancestors we seek,—and was told that the lowest vertebrate was Amphioxus, not Ammocœtes;

[1] *Proc. Cambridge Philos. Soc.*, vol. ix. p. 19, 1895.
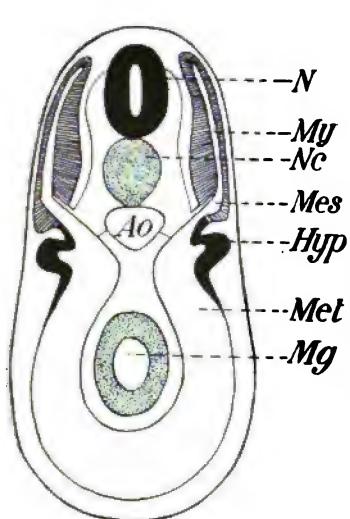
Fig. 3A.
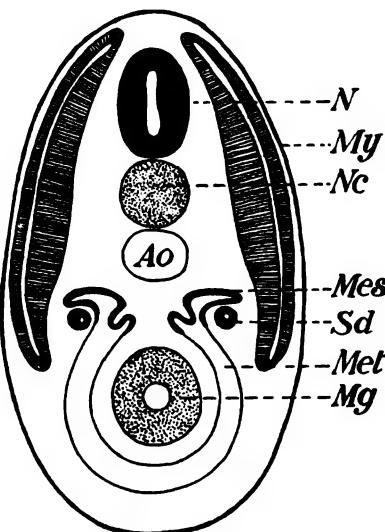
Fig. 3B.
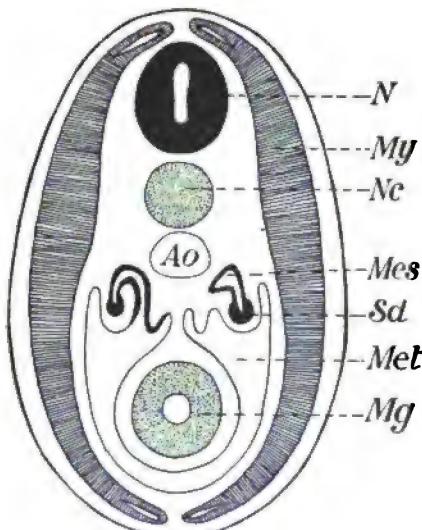
Fig. 3C.

FIG. 3—(after v. Wijhe).—*N.*, central nervous system ; *Nc.*, notochord ; *Ao.*, aorta ; *Mg.*, midgut.

    A.—*My.*, myocœle ; *Mes.*, mesocœle ; *Met.*, metacœle ; *Hyp.*, hypomer (pronephric).

    B. and C.—*My.*, myotome ; *Mes.*, mesonephros ; *S.d.*, segmental duct (pronephric) ; *Met.*, body cavity.

that therefore any argument as to the origin of vertebrates
must proceed from the consideration of the former and not the
latter animal.   My reply was then and is still, that I was
considering the cranial region in the first place, and that there-
fore it was necessary to take the lowest vertebrate which pos-
sessed cranial nerves and sense organs of a distinctly vertebrate
character, a criterion evidently not possessed by Amphioxus.
Such argument does not apply to the spinal region, so that,
now that I have left the cranial region and am considering the
spinal, I entirely agree with my critics that Amphioxus is likely
to afford valuable help, and ought to be taken into consideration
as well as Ammocœtes.   The distinction between the value
of the spinal (including respiratory) and cranial regions of
Amphioxus for drawing phylogenetic conclusions is recognised
by Boveri, who says[1] that, in his opinion, "Amphioxus shows
simplicity and undifferentiation rather than degeneration.   If
truly Amphioxus is somewhat degenerated, then it is so in its
prehensile and masticatory apparatus, its sense organs, and
perhaps its locomotor organs, owing to its method of living."

Hatschek describes in Amphioxus how the cœlom splits into
a dorsal segmented portion, the protovertebra, and a ventral un-
segmented portion, the lateral plates.   He describes in the
dorsal part the formation of myotome and sclerotome as in the
Craniota.   Also, just as in the latter case, the myotome is at
first confined to the dorsal region in the neighbourhood of the
spinal cord and notochord, and subsequently extends ventrally,
until, just as in Ammocœtes, the body is enveloped in a sheet
of somatic segmented muscles, the well known myomeres.

The conclusion is inevitable: any explanation of the origin
of the somatic muscles in Ammocœtes must also be an explana-
tion of the somatic muscles in Amphioxus, and conversely; so
that if in this respect Amphioxus is the more primitive and
simpler, then the condition in Ammocœtes must be looked
upon as derived from a more primitive condition, similar to
that found in Amphioxus.

Now, it is well known that a most important distinction
exists between Amphioxus and Ammocœtes in the topographical
relations of the ventral portion of this muscle sheet, for in the

[1] *Op. cit.*, p. 467.

former it is separated from the gut and the body cavity by the atrial space, while in the latter there is no such space. Für-bringer therefore concludes, as I have already mentioned,[1] that this space has become obliterated in the Craniota, but that it must be taken into consideration in any attempt at formulating the nature of the ancestors of the vertebrate.

Kowalewsky[2] described this atrial space as formed by the ventral downgrowth of pleural folds on each side of the body, which met in the mid-ventral line and enclosed the branchial portion of the gut. According to this explanation, the whole ventral portion of the somatic musculature of the adult Amphi-oxus belongs to the extension of the pleural folds, the original body musculature being confined to the dorsal region. This is expressed roughly on the external surface of Amphioxus by the direction of the connective tissue septa between the myotomes. These septa, as is well known, bend at an angle, the apex of which points towards the head. The part dorsal to the bend represents the part of the muscle belonging to the original body, the part ventral to the bend is the pleural part and represents the extension into the pleural folds.

Lankester and Willey[3] have attempted to give another ex-planation of the formation of the atrial cavity : they look upon it as originating from a ventral groove, which becomes a canal by the meeting of two outgrowths from the metapleure on each side. This canal then extends dorsalwards on each side, and so forms the atrial cavity; the metapleure still remains in the adult; the somatic muscles in the epipleure of the adult are the original body muscles, and not extensions into an epipleuric fold, for there is no such fold.

This explanation is a possible conception for the post-branchial portion of the atrium, but is impossible for the branchial region ; for, as Macbride[4] points out, as must necessarily be the case,

[1] Part III. of this series, "On the origin of the branchial segmentation," *This Journal*, vol. xxxiii. p. 183.

[2] "Weitere Stud. ü. d. Entwick. geschich. d. *Amphioxus lanceolatus*," *Arch. f. Mikr. Anat.*, Bd. xiii., 1877.

[3] "The development of the atrial chamber of Amphioxus," *Q. J. Micr. Sci.*, vol. xxxi., 1890.

[4] "Further remarks on the development of Amphioxus," by E. W. Macbride, *Q. J. Micr. Sci.*, vol. xliii. p. 357, 1900.

the point of origin of the atrial wall is in all stages of development situated at the end of the gill slit. It shifts in position with the position of the gill slit, but there can be no growing back of the cavity. Macbride therefore agrees with Kowalewsky that the atrial cavity is formed by the simultaneous ventral extension of pleural folds and of the branchial part of the original pharynx. Thus, in his summing up, he states:[1]

" 5. In the larva practically the whole sides and dorsal portion of the pharynx represent merely the hyperpharyngeal groove and the adjacent epithelium of the pharynx of the adult, the whole of the branchial epithelium of the adult being represented by a very narrow strip of the ventral wall of the pharynx of the larva. The subsequent disproportionate growth of this part of the pharynx of the larva and of the adjacent portion of the atrial cavity has given the impression that the atrial cavity grew upwards and displaced other structures, which is not the case."

Further, v. Wijhe[2] states that the atrium extends beyond the atriopore right up to the anus, just as must have been the case if the pleural folds originally existed along the whole length of the body. His words are: " Allerdings hat sich das Atrium beim Amphioxus lanceolatus eigenthümlich ausgebildet, indem sich dasselbe durch den ganzen Rumpf bis an den Anus, d. h. bis an die Wurzel des Schwanzes ansdehnt."

We get, therefore, this conception of the origin of the somatic musculature of the vertebrate. The invertebrate ancestor possessed on each side along the whole length of its body a lateral fold or pleuron which was segmented with the body and capable of movement with the body, because the dorsal longitudinal somatic muscles extended segmentally into each segment of the pleuron. By the ventral extension of these pleural folds not only was the smooth body surface of the vertebrate attained, but also the original appendages obliterated as such, leaving only as signs of their existence the branchiæ, the pronephric tubules, and the sense organs of the lateral line system.

Such an explanation signifies that the somatic trunk muscu-

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[1] *Op. cit.*, p. 359.

[2] " Beiträge z. Anat. der Kopfregion des *Amphioxus lanceolatus*," von J. W. van Wijhe, *Petrus Camper Deel.* 1, *Aflevering* 2, p. 59.

lature of the vertebrate was derived from the dorsal longitudinal musculature of the body of the arthropod, and not from the ventral longitudinal musculature, and that therefore the equivalent in the primitive arthropod stage of the myotome of the vertebrate did not give origin to the ventral longitudinal muscles of the invertebrate ancestor. Now, as I have said, v. Kennel states that in the procœlom of Peripatus a dorsal part (III. in fig. 1) is cut off which gives origin to the dorsal body musculature, while the ventral part which remains (I. and II. in fig. 1) gives origin in its appendicular portion (I.) to the muscles of the appendage, and presumably in its ventral somatic portion (II.) to the ventral longitudinal muscles of the body. This dorsal cut off part might be called the myotome, in the same sense as the corresponding part of the procœlom in the vertebrate is called the myotome. In both cases the muscles derived from it form only a part of the voluntary musculature of the animal, and in both cases the muscles in question are the dorsal longitudinal muscles of the body (to which must perhaps be added the dorso-ventral body muscles). Now, the whole of my theory on the origin of vertebrates arose from the investigation of the structure of the cranial nerves, which led to the conception that their grouping was not, like the spinal, a dual grouping of motor and sensory elements, but a dual grouping to supply two sets of segments, characterised especially by the different embryological origin of their musculature. The one set I called the somatic segmentation, because the muscles belonging to it were the great longitudinal body muscles; the other I called the splanchnic segmentation, because its muscles were those connected with the branchial and visceral arches. According to my theory, this latter segmentation was due to the segmentation of the appendages in the invertebrate ancestor; and in my previous papers, dealing as they do with the cranial region, attention was especially directed to the way in which the position of the striated splanchnic musculature could be explained by a transformation of the prosomatic and mesosomatic appendages. Now I am dealing with the metasomatic region, in which it is true the appendages take a very subordinate place, but still something corresponding to the splanchnic segments of the cranial region might fairly be expected to exist, and I

the conjoined nervous system and alimentary canal of the arthropod, then the vertebrate metacœle, or body cavity, must have been originally confined to the region on each side of the central nervous system, and from this position have spread ventrally to ultimately enclose the new formed vertebrate gut. This means that the body cavity (metacœle) of the vertebrate is not the same as the body cavity of the annelid, but corresponds to a ventral extension of the nephrocœle, or ventral part of such body cavity.

Such a phylogenetic history is most probable, because it explains most naturally and simply the facts of the development of the vertebrate body cavity; for the mesoblast always originates in the neighbourhood of the notochord and central nervous system, and the lumen of the body cavity always appears first in that region, and then extends laterally and ventrally on each side until it reaches the most ventral surface of the embryo, thus forming a ventral mesentery, which ultimately disappears, and the body cavity surrounds the gut, except for the dorsal mesentery. Thus Shipley [1] in his description of the formation of the mesoblastic plates which line the body cavity in Ammocœtes describes them as commencing in two bands of mesoblast situated on each side, close against the commencing nervous system : " these two bands [2] are separated dorsally by the juxtaposition of the dorsal wall of the mesenteron and the epiblast, and ventrally by the hypoblastic yolk-cells which are in contact with the epiblast over two-thirds of the embryo. Subsequently, but at a much later date, the mesoblast is completed ventrally by the downgrowth on each side of these mesoblastic plates. The subsequent downward growth is brought about by the cells proliferating along the free ventral edge of the mesoblast; these cells then growing ventralwards, pushing their way between the yolk-cells and epiblast."

The derivation of the vertebrate pronephric ̤ segmental organs from the metasomatic coxal glands of a primitive arthropod would mean, if the segmental organs of Peripatus be taken as the type, that such glands opened to the exterior on

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[1] " On some points in the development of *Petromyzon fluviatilis*," by A. E. Shipley, *Q. J. Micr. Sci.*, 1887.

[2] *Op. cit.*, pp. 5 and 6, fig. 16.

every segment, either at the base of the appendage or on the appendage itself.

It is taken for granted by most observers that the pronephric segmental organs once opened to the exterior on each segment, and then, from some cause or other, ceased to do so, and the separate ducts, by a process of fusion, came to form a single segmental duct, which opened into the cloaca. Many observers have been led to the conclusion that the pronephric duct is epiblastic in origin, although, from its position in the adult, it appears far removed from all epiblastic formations. However, at no time in the developmental history is there any clear evidence of actual fusion of any part of the pronephric organ with the epidermis, and the latest observer, Brauer, is strongly of opinion that there is never sufficiently close contact with the epidermis to warrant the statement that the epiblastic cells take part in the formation of the duct. All that can be said is, that the formation of the duct takes place at a time when the pronephric diverticulum is in close propinquity to the epidermis, before the ventral downgrowth of the myotome has taken place.

The formation of the anterior portion of the pronephric duct is, according to Maas[1] in Myxine, and Wheeler[2] in Petromyzon, undoubtedly formed by the fusion of a number of pronephric tubules, which, according to Maas, are clearly seen in the youngest specimens as separate segmental tubes; each of these tubules is supplied by a capillary network from a segmental branch of the aorta, as in the tubules of Amphioxus according to Boveri, and does not possess a glomerulus.

The posterior part of the duct into which the mesonephric tubules enter possesses also a capillary network, which Maas considers to represent the original capillary network of a series of pronephric tubules, the only remnant of which is the duct into which the mesonephric tubule opens. He therefore argues that the pronephric duct indicates a series of pronephric tubules, which originally extended along the whole length of the body,

[1] Op. cit.
[2] " Development of the urinogenital organs of the Lamprey," by Wheeler, Zool. Jahrbuch, Bd. xiii. p. 1, 1899.

For my own part I should expect to find evidence of a
former existence of an atrial cavity rather in the pigment
round the pronephros and its duct than in the duct itself.

The conception that Amphioxus shows us how to account
for the great envelope of somatic muscles which wraps round
the vertebrate body, in that the ancestor of the vertebrate
possessed on each side of the body a segmented pleuron, is
exactly in accordance with the theory of the origin of verte-
brates deduced from the study of Ammocœtes, as already set
forth in this series of papers; for we see that one of the
striking characteristics of such forms as Bunodes, Hemiaspis,
etc. is the presence on each side of the main part of the body
of segmented pleural flaps; and if we pass further back to the
great group of Trilobites, we find in the most manifold form and
in various degrees of extent the most markedly segmented
pleural folds. In fact the hypothetical figure (fig. 4A) which
I have deduced from the embryological evidence might very
well represent a cross section of a trilobite, provided only that
each appendage of the trilobite possessed an excretory coxal
gland.

The earliest fishes, then, ought to have possessed segmented
pleural folds, which were moved by somatic muscles, and
enveloped the body after the fashion of Ammocœtes and
Amphioxus, and I cannot help thinking that Cephalaspis
shows in this respect also its relation to Ammocœtes. It is
well known that some of the fossil representatives of the
Cephalaspids show exceedingly clearly that these animals
possessed a very well segmented body, and it is equally recog-
nised that this skeleton is a calcareous, not a bony skeleton, and
does not represent vertebræ, etc. It is generally called an
aponeurotic skeleton, meaning thereby that what is preserved
represent not dermal plates alone or a vertebrate skeleton, but
the calcified septa or aponeuroses between a number of muscle
segments or myomeres, precisely of the same kind as the septa
between the myomeres in Ammocœtes. The termination of
such septa on the surface would give rise to the appearance of
dermal plates or scutes, or even the septa may have been attached
to something of the nature of dermal plates. The same kind of
picture would be represented if these connective tissue dis-

sepiments of Ammocœtes were calcified, and then the animal was fossilised. In agreement with this interpretation of the spinal skeleton of Cephalaspis, it may be noted that again and again in parts of these dissepiments I have found in old specimens of Ammocœtes nodules of cartilage formed, and at transformation it is in this very tissue that the spinal cartilages are formed.

FIG. 5A.
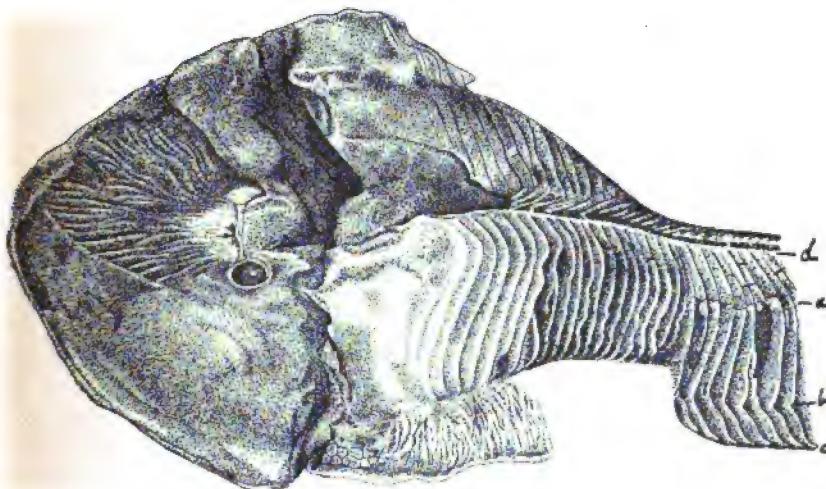
FIG. 5B.

FIG. 5A.[1]—Facsimile of Woodward's drawing of a specimen of *Cephalaspis Murchisoni*, as seen from the side. The cephalic shield is on the right and caudal to it the pleural fringes are well shown.

B.—Another specimen of *Cephalaspis Murchisoni* taken from the same block of stone, showing the dermo-septal skeleton and in one place the pleural fringes, *bc.*

Now, the specimens of Cephalaspis all show, as seen in fig. 5, that the skeletal septa cover the body regularly, and then along one line are bent away from the body to form as it were

[1] *British Museum Catalogue of Fossil Fishes*, by A. S. Woodward, part ii. pl. x. fig. 1. London, 1891.

a fringe, or rather a free pleuron, which has been easily pushed
at an angle to the body skeleton in the process of fossilisation.
I had the pleasure of seeing Prof. Patten in Cambridge this last
summer (1901), and he drew my attention especially to this
fringed edge.   He thinks it is evidence of a number of segmental
appendages which were jointed to the corresponding body seg-
ments, and in the best specimen at the South Kensington Natural
History Museum he thinks such joints are clearly visible.   He
concludes, therefore, that the Cephalaspids were Arthropods,
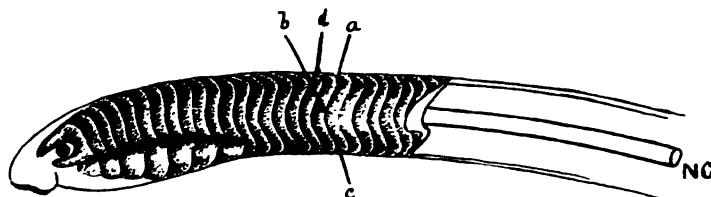
FIG. 6A.
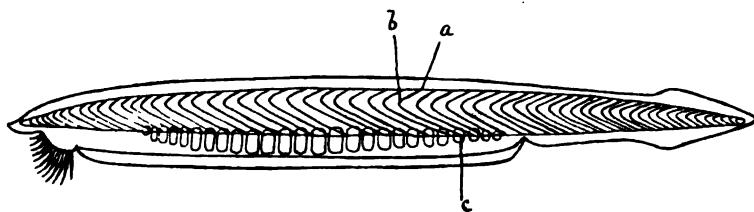
FIG. 6B.

FIG. 6A.—Arrangement of septa in Ammocœtes.   *NC*, position of notochord.
    B.—Arrangement of septa in Amphioxus.

and not Vertebrates.   I have also carefully examined this
specimen, and do not consider that what is seen resembles the
joint of an arthropod appendage; the appearance is rather such
as would be produced if the line of attachment of Patten's
appendages to the body was the place where the pleural body
folds became free from the body, and so with any pressure a
bending or fracture of the calcified plates would take place along
this line.

     There is undoubtedly an appearance of finish at the termina-
tion of these skeletal fringes, as though they terminated in a
definitely shaped spear-like point, just as is seen in the trilobite

pleuræ. This again, to my mind, is rather evidence of pleural fringes than of true appendages.

As already argued, I look upon Ammocœtes as the only living fish at all resembling the Cephalaspids; it is therefore instructive to compare the arrangement of this spinal dermo-septal skeleton of Cephalaspis with that of the septa between the myomeres in the trunk region of Ammocœtes and Amphioxus. Such a skeleton in Ammocœtes would be represented by a series of plates overlapping each other, arranged as in fig. 6A, and in Amphioxus as in fig. 6B. I have lettered the corresponding parts of the two structures by similar letters, a, b, c. Ammocœtes differs in configuration from Amphioxus in. that it possesses an extra dorsal (a d) and an extra ventral bend. Ammocœtes is a much rounder animal than the Amphioxus, and both the dorsal and ventral bends are on the extreme ventral and dorsal surfaces, surfaces which can hardly be said to exist in Amphioxus. The part, then, of such an aponeurotic skeleton of Ammocœtes which I imagine corresponds to b c in Amphioxus, and therefore would represent the pleural fold, is the part ventral to the bend at b. In both animals this bend corresponds to the position of the notochord NC.

The skeleton of Cephalaspis compares more directly with that of Ammocœtes than of Amphioxus, for there is the same extra dorsal bend (a d) as in Ammocœtes; the lateral part of the skeleton again gives an angle a b c; the part from b to c would therefore represent the pleural fold. I picture to myself the sequence of events somewhat as follows:

First, a protostracan ancestor, which like Peripatus possessed appendages on every segment into which cœlomic diverticula passed, forming a system of coxal glands. Such glands being derived from the segmental organs of the Chætopods, originally discharged to the exterior by separate openings on each segment; it is, however, possible, and I think probable, that a fusion of these separate ducts had already taken place in the protostracan stage, so that there was only one external opening for the whole of these metasomatic coxal glands, just as there is only one external opening for the corresponding prosomatic coxal glands of Limulus. Then, by the ventral growth of pleural body folds, such appendages became enclosed and useless, and the coxal

glands of the post-branchial segments, with their segmental or pronephric duct, were all that remained as evidence of such appendages. This dwindling of the metasomatic appendages was accompanied with the getting rid of free appendages generally, in the manner set forth in these papers, and so a smooth fish-like body surface was formed; then came elongation for the purpose of increasing mobility by the addition of segments between those last formed and the cloacal region; each of such new formed segments was appendageless, so that its segmental organ was not a coxal gland, but entirely somatic in position: formed, therefore, a mesonephric tubule, not a pronephric one. Such glands could no longer excrete to the exterior, owing to the exclosing shell of the pleural folds, but the pronephric duct was there, already formed, and so these nephric tubules opened into that, instead of, as in the case of the branchial slits, forcing their way through the pleural walls when the atrium became closed.

The Meaning of the Ductless Glands.

If it is a right conception, that the excretory organs of the protostracan group, which gave origin to the vertebrates as well as to the crustaceans and arachnids, were of the nature of coxal glands, then it follows that such coxal glands must have existed originally on every segment, because they themselves were derived from the segmental organs of the annelids, and it is therefore worth making an attempt to trace the fate of such segmental organs in the Vertebrate as well as in the Crustacean and Arachnid.

Such an attempt is possible, it seems to me, because there exists throughout the animal kingdom striking evidence that excretory organs which no longer excrete to the exterior do not disappear, but still perform excretory functions of a different character. Their cells still take up effete or injurious substances, and instead of excreting to the exterior, excrete into the blood, forming either ductless glands of special character, or glands of the nature of lymphatic glands.

The problem presented to us is as follows:—

The excretory organs of both arthropods and vertebrates

arose from those of annelids, and were therefore originally present in every segment of the body. In most arthropods and vertebrates they are present only in certain regions, in the former case as the coxal glands of the prosomatic or head region, in the latter as the nephric glands of the metasomatic or trunk region, and in the case of Amphioxus of the mesosomatic or branchial region.

In the original arthropod, judging from Peripatus, they were present, as in the annelid, in all the segments of the body, and formed coxal glands.

Therefore, in the ancestors of the living Crustacea and Arachnida, coxal glands must have existed in all the segments of the body, and we ought to be able to find the vestiges of them in the mesosomatic or branchial and metasomatic or abdominal regions of the body.

Similarly in the vertebrates, derived, as has been shown, not from the annelids, but from an arthropod stock, evidence of the previous existence of coxal glands ought to be manifested in the prosomatic or trigeminal region, in the mesosomatic or branchial region, as well as in the metasomatic or post-branchial region.

How does an excretory organ change its character when it ceases to excrete to the exterior? what should we look for in our search after the lost coxal glands?

The answer to these questions is most plainly given in the case of the pronephros, especially in Myxine, where Maas[1] has been able to follow out the whole process of the conversion of nephric tubules into a tissue resembling that of a lymph gland.

He states, in the first place, that the pronephros possesses a capillary network, which extends over the pronephric duct, while the tubules of the mesonephros possess not only this capillary network, equivalent to the capillaries over the convoluted tubules in the higher vertebrates, but also a true glomerulus, in that the nephric segmental arteriole forms a snarl (knauel), and pushes in the wall of the mesonephric tubule (see fig. 28, pl. xli.). He describes[2] the pronephros of large adult individuals as consisting of—

1. Tubules with funnels which open into the pericardial cœlom.

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[1] *Op. cit.*　　　　　　　　　　[2] *Ibid.,* p. 486.

2. A large capillary network (the glomus) at the distal end.

3. A peculiar tissue (the strittige Gewebe of the Semon-Spengel controversy), which Spengel considers to be composed of the altered epithelium of pronephric tubules, while Semon looks on it as an amalgamation of glomeruli.

Maas is entirely on the side of Spengel, and shows that this peculiar tissue is actually formed by modified pronephric tubules, which become more and more lymphatic in character.

He says:[1] "The pronephros consists of a number of nephric tubules, placed separately one behind the other, which were originally segmental in character, each one of which is supplied by a capillary network from a segmental branch of the aorta. The tubules begin with many mouths (dorso-lateral and medial-ventral) in the pericardial cavity; on their other blind end they have lost their original external opening, and there, in the cranial portion of the head kidney, before they have joined together to form a collecting duct, they, together with the vascular network, are transformed into a peculiar adrenal-like tissue. The most posterior of the segmental capillary nets retain their original character, and are concentrated into the separate capillary mass known as the glomus."

Later on[2] he says: "Further, the separate head kidney is more and more removed in structure from an excretory organ in the ordinary sense. One cannot, however, speak of it as an organ becoming rudimentary; this is proved not only by the progressive transformation of its internal tissue into a tissue of a very definite character, but also by the cilia in its canals and the steady increase in the number of its funnels. It appears, therefore, to be the conversion of an excretory organ into an organ for the transference of fluid out of the coelom into a special tissue, i.e. into its blood sinus; in other words, into an organ which must be classed as belonging to the lymph system."

In exact correspondence with this transformation of a nephric tubule into a ductless gland of the nature of a lymphatic gland, is the formation of the head kidney in Teleosteans. Thus Weldon points out[3] that "though the observations of Balfour

[1] *Ibid.*, p. 497.   [2] *Ibid.*, p. 504.

[3] "On the suprarenal bodies of Vertebrates," by W. F. R. Weldon, *Q. J. Micr. Sci.*, vol. xxv. p. 147.

left it highly probable that the 'lymphatic' tissue described by him was really a result of the transformation of part of the embryonic kidney, he did not investigate the details of its development. This was afterwards done by Emery,[1] with the following results.

"In those Teleostei which he has studied, Professor Emery finds that at an early stage the kidney consists entirely of a single pronephric funnel, opening into the pericardium, and connected with the segmental duct, which already opens to the exterior. Behind this funnel, the segmental duct is surrounded by a blastema, derived from the intermediate cell mass, which afterwards arranges itself more or less completely into a series of solid cords, attaching themselves to the duct. These develop a lumen and become normal segmental tubules, but it is, if I may be allowed the expression, a matter of chance how much of the blastema becomes so transformed into kidney tubules, and how much is left as the 'lymphatic' tissue of Balfour, this 'lymphatic' tissue remaining either in the pronephros only, or in both pro- and meso-nephros."

If we turn now to the invertebrates, we see also how close a connection exists between lymphatic and phagocytic organs and excretory organs. The chief merit for this discovery is due to Kowalewsky, who, taking a hint from Heidenhain's work on the kidney, in which he showed how easy it was to find out the nature of different parts of the mammalian excretory organ by the injection of different substances, such as a solution of ammoniated carmine or of indigo-carmine, has injected into a large number of different invertebrates various colouring matters, or litmus, or bacilli, and thus shown the existence not only of known excretory organs, but also of others, lymphatic or lymphoid in nature, not hitherto suspected.

In all cases he finds that a phagocytic action with respect to solid bodies is a property of the leucocytes, that these leucocytes which are found in the coelomic spaces of the Annelida, etc. are apparently derived from the epithelium of such spaces, that by the proliferation of such epithelium in places, e.g. the septal glands of the terrestrial Oligochæta, segmental glandular masses of such tissue are formed which take up the colouring matter,

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[1] *Alti dell' Acad. d. Lincei*, 1882.

etc. That in the limicolous Oligochæta such septal glands are not found, but that at the commencement of the nephridial organ, immediately following upon the funnel, a remarkable modification of the nephridial wall takes place to form a large cellular cavernous mass, the so-called filter, which in Euaxes is full of leucocytes, the cells are only definable by their nuclei, and look like and act in the same way as the free leucocytes outside this nephridial appendage. As G. Schneider[1] points out, the whole arrangement is very like that described by Kowalewsky[2] in the leeches Clepsine and Nephelis, where, also immediately succeeding the funnel of the nephridial organ, a large accessory organ is found, which is part of the nephridium, and is called the nephridial capsule. This is the organ *par excellence* which takes up the solid carmine grains, bacillus, etc., and apparently, from Kowalewsky's description, contains leucocytes in large numbers.

We see, then, that in such invertebrates, just as in the vertebrate, modifications of the true excretory organ may give rise to phagocytic glands of the nature of lymphatic glands.

Further, these researches of Kowalewsky suggest in the very strongest manner that whenever by such means new, hitherto unsuspected glands are discovered, such glands must belong to the excretory system, *i.e.* must be derived from cœlomic epithelium, even when all evidence of any cœlom has disappeared. Kowalewsky himself was evidently so impressed with the same feeling that he heads one of his papers[3] "The excretory organs of the Pantopoda," although the organs in question have been discovered by him by this method, and appeared as ductless glands with no external opening.

To my mind these observations of Kowalewsky are of exceeding interest, for it is immediately clear that if the segmental organs of the annelids, which must have existed on all the segments of the forefathers of the crustacea and arachnida (the Protostraca),

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[1] "Ueber phagocytäre Organe und Chloragogenzellen der Oligochæta," v. G. Schneider, *Zeit. f. wiss. Zool.*, Bd. 61, p. 363, 1896.

[2] "Étude Biologique sur les Clepsines," *Mém. de l'Acad. Imp. d. Sci. de St Petersbourg*, viii. sér., 1897.

[3] "Ein Beitrag zur Kenntniss der Excretionsorgane der Pantopoden," von A. Kowalewsky, *Mém. d. l'Acad. Imp. d. Sci. d. St 'Petersbourg*, vii. sér., vol. xxxviii., 1890.

have left any sign of their existence in living crustaceans and arachnids, then such indication would most likely take the form of lymphatic glands in the places where the excretory organs ought to have been.

Now, as already pointed out in Peripatus, such segmental organs were formed by the ventral part of the cœlom, and dipped originally into each appendage; also we know that each segment of an arachnid embryo possesses a cœlomic cavity in its ventral part which extends into the appendage on each side; this cavity afterwards disappears, and is said to leave no trace in the adult of any excretory coxal gland derived from its walls. If, however, it is found that in the very position where such organ ought to have been formed a segmentally arranged ductless gland is situated, the existence of which is shown by its taking up of carmines, etc., then it seems to me that in all probability such gland is the modification of the original coxal gland.

This is what Kowalewsky[1] has done. Thus he states that Metschnikoff had fed *Mysis* with carmine grains, and found tubules at the base of the thoracic feet coloured red with carmine. He himself used an allied species, *Paropodopsis cornutum*, and found here also that the carmine was taken up by tubules situated in the basal segments of the feet.

In *Nebalia*, feeding experiments with alizarin blue and carmine stained the antennal glands, and showed the existence of glands at the base of the eight thoracic feet. These glands resemble the foot glands of Mysis, Parapodopsis, and Palæmon, and lie in the space through which the blood passes from the thoracic feet, *i.e.* from the gills to the heart.

In *Squilla* also, in addition to the shell glands, special glands were discovered on the branchial feet on the path of the blood to the heart. These glands form continuous masses of cells which constitute large compact glands at the base of the branchial feet. Single cells of the same sort are found along the whole course of the branchial venous canal, right up to the pericardium.

These observations show that the Crustaceans possess not only true excretory organs in the shape of coxal glands, *i.e.* antennary glands, shell glands, etc., in the cephalic region, but also a series

[1] "Ein Beitrag zur Kenntniss der Excretionsorgane," *Biologisches Central-blatt,* 1889.

of segmental glands situated at the base of the appendages, especially of the respiratory appendages:—a system, that is to say, of coxal glands which had lost their excretory function, having lost their external opening, but had not in consequence disappeared, but still remained *in situ*, and still retained an important excretory function, having become lymphatic glands containing leucocytes. Such are especially found in the branchial appendages, and are called by Cuénot,[1] who describes them for all Decapods, as branchial glands.

Further, it is significant that the same method reveals the existence in Pantopods[2] of a double set of glands of similar character, one set in the basal segments of the appendages and the other in the adjacent part of the body.

Also in scorpions, Kowalewsky[3] has shown that the remarkable lymphatic organ situated along the whole length of the nerve cord in the abdominal region takes up carmine grains and bacilli, an organ which in Androctonus does not form one continuous gland, but a number of separate apparently irregularly grouped glandular bodies.

In addition to this median lymphatic gland, Kowalewsky has discovered in the scorpion a pair of lateral glands, to which he gives the name of lymphoid glands, which communicate with the thoracic body cavity (*i.e.* the pseudo-cœle), are phagocytic, and according to him give origin to leucocytes by the proliferation of their lining cells, thus, as he remarks, reminding us of the nephridial capsules of Clepsine. These glands are so closely related in position to the coxal glands on each side, that he has often thought that the lumen of the gland communicated with that of the coxal gland; he, however, has persuaded himself that there is no true communication between the two glands.

Neither of these organs appear to be segmental, and until we know how they are developed, it is not possible to tell whether they represent fused segmental organs or not.

The evidence, then, is very strong that in the Crustacea and

[1] " Études sur le sang et les glandes lymphatiques dans la série animale " (2nd partie : invertébrés), par L. Cuénot, *Arch. d. Zool. exper. gen.*, 2 sér. T. 9, 1891.　　　　　　　　　　　　　　　　　[2] *Op. cit.*

[3] " Une nouvelle glande lymphatique chez le scorpion d'Europe," par A. Kowalewsky, *Mém. d. l'Acad. Imp. d. Sci. d. St Petersbourg*, viii. sér., vol. v., 1897.

Arachnida the original segmental excretory organs do not disappear, but remain as ductless glands, of the nature of lymphatic glands, which supply leucocytes to the system.

Further, the evidence shows that the nephric organs, or parts of the cœlom in close connection with these organs, may be transformed into ductless glands, which do not necessarily contain free leucocytes like lymph glands, but yet are of such great importance as excretory organs that their removal profoundly modifies the condition of the animal. Such a gland is the so-called adrenal or suprarenal body, disease of which is a feature of Addison's disease; a gland which forms and presumably passes into the blood a substance of remarkable power in causing contraction of blood-vessels, a substance which has lately been extracted in crystalline form by Jokichi Takamine,[1] and called by him 'adrenalin': a gland, therefore, of very distinct peculiar properties, which cannot be regarded as rudimentary, but as of vital importance for the due maintenance of the healthy state.

In the Elasmobranchs two separate glandular organs have been called suprarenal, a segmental series of paired organs, each of which possesses a branch of the aorta and a sympathetic ganglion, and an unpaired series in close connection with the kidneys, to which Balfour gave the name of interrenal glands.

Of these two sets of glands, Swale Vincent has shown that the extract of the interrenals has no marked physiological effect, in this respect resembling the extract of the cortical part of the mammalian gland, while the extract of the paired segmental organs of the Elasmobranch produces the same remarkable rise of blood pressure as the extract of the medullary portion of the mammalian gland.

Also the development of these two sets of glands is asserted to be different. Balfour considered that the suprarenal were derived from sympathetic ganglion cells, but left the origin of the interrenal doubtful. Weldon [2] showed that the cortical part of the suprarenals in the lizard was derived from the wall of the glomerulus of a number of mesonephric tubules. In Pristiurus,

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[1] "The isolation of the active principle of the suprarenal gland," by Jokichi Takamine, *Proc. of the Physiol. Soc.*, Dec. 14, 1901 : *Journ. of Physiol.*, vol. xxvii.   [2] *Op. cit.*

he stated that the mesoblastic rudiment described by Balfour as giving origin to the interrenals is derived from a diverticulum of each segmental tubule, close to the narrowing of its funnel-shaped opening into the body cavity. With respect to the paired suprarenals he was unable to speak positively, but doubted whether they were derived entirely from sympathetic ganglion.

Weldon sums up the results of his observations by saying[1] "that all Vertebrates except Amphioxus have a portion of the kidney modified for some unknown purpose not connected with excretion; that in Cyclostomes the pronephros alone is so modified, in Teleostei the pro- and part of the meso-nephros; while in the Elasmobranchs and the higher Vertebrates, the mesonephros alone gives rise to this organ, which has also in these forms acquired a secondary connection with certain of the sympathetic ganglia."

Since Weldon's paper, a large amount of literature on the origin of the adrenals has appeared, a summary of which up to 1891 is given by Hans Rabl[2] in his paper, and a further summary by Aichel[3] in his paper published in 1900. The result of the investigations up to this latter paper may be summed up by saying that the adrenals, using this term to include all these organs of whatever kind, are in all cases partly at all events derived from some part of the walls of either the mesonephric or pronephric excretory organs, but that in addition a separate origin from the sympathetic nervous system must be ascribed to the medullary part of the organ and to the separate paired organs in the Elasmobranchs, which are equivalent to the medullary part in other cases.

I must say that I cannot believe in the transformation of nerve cells into a glandular organ, and therefore am very pleased to find that Aichel's observations show that such is not the case, but that the suprarenals of Elasmobranchs are in the earliest stage derived from the transverse portion of the mesonephric

[1] "Note on the origin of the suprarenal bodies in Vertebrates," *Proc. Roy. Soc.*, vol. xxxvii. p. 424, 1884.
[2] "Die Entwick. u. Struct. d. Nebennieren b. d. Vögeln," von Hans Rabl, *Arch. f. Mikr. Anat.*, Bd. xxxviii. p. 492, 1891.
[3] "Vergleich. Entwick. geschich. u. Stam. geschich. d. Nebennieren," von O. Aichel, *Arch. f. Mikr. Anat.*, vol. lvi. p. 1, 1900.

tubules which have lost their connection with the epithelium of the body cavity, the funnel of these tubules disappearing. Soon a sympathetic ganglion comes into close contact with this modified nephric diverticulum, and so the adult organ is formed.

He also states that the interrenals are formed before the suprarenals, and commence at a time when the mesonephric tubule has not yet become joined to the segmental duct. They commence as a cellular protuberance on the inner wall of the mesonephric funnel.

In higher vertebrates (Rodents, etc.) Aichel finds that the adrenals arise in close connection with the mesonephric funnels; the sympathetic ganglia have no connection at first, but come later into close contact with the adrenals; there is no reason to suppose that any part of the glandular substance is derived from the modification of nerve cells. As he says, he entirely agrees with and confirms Weldon's point of view.

It is to my mind especially interesting to notice how, according to both Weldon and Aichel, the adrenals, or at all events the interrenals, arise from the same part of the nephric tubule as the nephridial capsules described in Kowalewsky's papers[1] for both leeches and certain worms:—In all cases a bulging of the wall of the nephridium close to its funnel-shaped opening into the body cavity.

Swale Vincent[2] appears to object strongly to Aichel's statements on the ground of his physiological experiments as to the action of suprarenal extract, the activity being confined to the medullary portion of the mammalian gland, and to the paired suprarenals of the elasmobranch, always in fact to the part of the gland containing sympathetic nerve cells; and he says that the evidence of Leydig, Balfour, etc. for the origin of the medullary part from sympathetic cells is so strong, and the physiological evidence of a difference of origin of the two parts of the gland so convincing, that he does not imagine that many morphologists or physiologists will be found to accept Aichel's teaching. I should have thought myself that no physiologist would accept the doctrine of the conversion of nerve cells into glandular tissue, and would be glad therefore to find that it was not necessary to do so; such appears also to have been previously the opinion of

[1] *Op. cit.* [2] *Anat. Anzeiger*, Bd. xviii., 1900, p. 74.

Swale Vincent, for, talking of the segmental suprarenal bodies of the elasmobranch, he says,[1] "I am inclined to think that the connection between the sympathetic nervous system and these bodies has been overstated. They are intimately involved in the sympathetic plexuses, and often have tiny ganglia very close to them; but in the adult, at any rate, whatever their developmental relations may be, *it can, in my opinion, not be truly said that they are an integral part of the sympathetic nervous system.*"[2]

The evidence, then, of the transformation of the known vertebrate excretory organs—the pronephros and the mesonephros—leads to the conclusion that in our search for the missing coxal glands of the meso- and pro-somatic regions we must look for either lymphatic glands or ductless glands of distinct importance to the body. I have already considered the question in the prosomatic region,[3] and have given my reasons why the pituitary gland must be looked upon as the descendant of the arthropod coxal gland. In this case also the resulting ductless gland is still of functional importance, for disease of it is associated with acromegaly. If, as is possible, it is homologous with the Ascidian hypophysial gland, then it is confirmatory evidence that this latter is said by Julin to be an altered nephridial organ.

Finally, I come to the mesomatic or branchial region; and here, strikingly enough, we find a perfectly segmental glandular organ of mysterious origin—the thymus gland—segmental with the branchiæ, not necessarily with the myotomes, belonging therefore to the appendicular system; and since the branchiæ represent, according to the theory, the basal part of the appendage, such segmental glands would be in position coxal glands. Here, then, in the thymus may be the missing mesosomatic coxal glands.

What, then, is the thymus?

The answer to this question has been given recently by Beard,[4] who strongly confirms Kölliker's original view that the

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[1] "Contributions to the comparative anatomy and histology of the suprarenal capsules," by Swale Vincent, *Trans. Zool. Soc. Lond.*, vol. xiv., part iii., 1897, p. 53.   [2] The italics are Swale Vincent's.

[3] Part VI. of this series of papers: "The old mouth and the olfactory organ: meaning of the pituitary body," *This Journal*, vol. xxxiv. p. 532.

[4] "The source of leucocytes and the true function of the thymus," *Anat. Anzeiger,* vol. xviii. p. 550, 1900.

thymus is a gland for the manufacture of leucocytes, and that such leucocytes are directly derived from the epithelium cells of the thymus. Kölliker also further pointed out that the blood of the embryo is for a certain period destitute of leucocytes.

Beard confirms this last statement, and says that up to a certain stage (varying from 10–16 mm. in length of the embryo) the embryos of *Raja batis* have no leucocytes in the blood or elsewhere; up to this period the thymus placode is well formed, and the first leucocytes can be seen to be formed in it from its epithelial cells; then such formation takes place with great rapidity, and soon an enormous discharge of leucocytes occurs from the thymus into the tissue spaces and blood; he therefore concludes that all lymphoid tissues in the body arise originally from the thymus gland, *i.e.* from leucocytes discharged from the thymus.

The segmental branchial glands known by the name of thymus are, according to this view, the original lymphatic glands of the vertebrate, and it is to be noted that in fishes and in amphibia lymphatic glands, such as we know them in the higher mammals, do not exist; they are characteristic of the higher stages of vertebrate evolution. In the lower vertebrates the only glandular masses apart from the cell lining of the body cavity itself, which give rise to leucocyte-forming tissue, are these segmental branchial glands, or possibly also the modified post-branchial segmental glands, known as the head kidney in Teleosteans, etc.

The importance ascribed by Beard to the thymus in the formation of leucocytes in the lowest vertebrates would be considerably reduced in value if the branchial region of Ammocœtes possessed neither thymus glands nor anything equivalent to them. Such, however, is not the case; Schaffer[1] has shown that in the young Ammocœtes masses of lymphatic glandular tissue are found segmentally arranged in the neighbourhood of each gill slit, tissue which soon becomes converted into a swarming mass of leucocytes, and shows by its staining, etc. how different it is from a blood space. The presence of this thymus leucocyte-forming tissue, as described by Schaffer, is

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[1] " Ueber die Thymusanlage bei Petromyzon Planeri," von J. Schaffer, *Sitzingsber. d. Kais. Akad. d. Wiss. in Wien*, Bd. 103, 1894.

confirmed by Beard, and I myself have seen the same thing in my youngest specimen of Ammocœtes.

Further, the very methods by which Kowalewsky has brought to light the segmental lymph glands of the branchial region of the Crustacea, etc., are the same as those by which Weiss[1] discovered the branchial nephric glands in Amphioxus: excretory organs which Boveri[2] considers to represent the pronephros of the Craniota. In this supposition Boveri is right in so far that both pronephros and the tubules in Amphioxus belong to the same system of excretory organs, but I entirely agree with v. Wijhe[3] that the region in Amphioxus is wrong. The tubules in Amphioxus ought to be represented in the branchial regions of the Craniota, not in the post-branchial region; v. Wijhe therefore[4] suggests that further researches may homologise them with the thymus gland in the Craniota, not with the pronephros.

This suggestion of v. Wijhe appears to me a remarkably good one, especially in view of the position of the thymus glands in Ammocœtes and the nephric branchial glands in Amphioxus. If, as I have pointed out, the atrial cavity of Amphioxus has been closed in Ammocœtes by the apposition of the pleural fold with the branchial body surface, then the remains of the position of the atrial chamber must exist in Ammocœtes as that extra-ordinary space between the somatic muscles and the branchial basketwork filled with blood spaces and modified muco-cartilage. It is in this very space close against the gill slits where the thymus glands of Ammocœtes are found, in the very place where the nephric tubules of Amphioxus would be found if its atrial cavity were closed completely. Instead, therefore, of considering with Boveri that the branchial nephric tubules of Amphioxus still exist in the Craniota as the pronephros, and that the atrial chamber has narrowed down to the pronephric duct, I would agree with v. Wijhe that the pronephros is post-branchial, and suggest that by the complete closure of the atrial space in the branchial region the branchial nephric tubules

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[1] *Op. cit.*   [2] *Op. cit.*

[3] "Beiträge z. Anat. u. der Kopfregion des *Amphioxus lanceolatus*," von J. W. van Wijhe, *Petrus Camper Deel.* 1, *Aflevering* 2.

[4] *Op. cit.*, p. 58.

have lost all external opening, and consequently, as in all other cases, have changed into lymphatic tissue and become the segmental thymus glands.

As v. Wijhe himself remarks, the time is hardly ripe for making any positive statement about the relationship between the thymus gland and branchial excretory organs. There is at present not sufficient consensus of opinion to enable us to speak with any certainty on the subject, yet there is so much suggestiveness in the various statements of different authors as to make it worth while to consider the question briefly.

On the one hand, thymus, tonsils, parathyroids, epithelial cell nests and parathymus are all stated to be derivatives of the epithelium lining the gill slits, and Maurer [1] would draw a distinction between the organs derived from the dorsal side of the gill cleft and those derived from the ventral side; the former being thymus, the latter forming the (epithelial Körper) epithelial cell nests, *i.e.* parathyroids. The thymus in Ammocœtes, according to Schaffer, lies both ventral and dorsal to the gill cleft; Maurer thinks that only the dorsal part corresponds to the thymus, the ventral part corresponding to the parathyroids, etc. Structurally, the thymus, parathyroids and the epithelial cell nests are remarkably similar, so that the evidence appears to point to the conclusion that in the neighbourhood of the gill slits segmentally arranged organs of a lymphatic character are situated, which give origin to the thymus, parathyroids, tonsils, etc.

Now among these organs, *i.e.* among the ventrally situated ones, Maurer places the carotid gland, so that if he is right, the origin of the carotid gland might be expected to help in the elucidation of the origin of the thymus.

The origin of the carotid gland has been investigated recently by Kohn,[2] who finds that it is associated with the sympathetic nervous system in the same way as the suprarenals. He desires, in fact, to make a separate category for such nerve glands, or paraganglia, as he calls them, and considers them all to be derivatives of the sympathetic nervous system, and nothing to

[1] " Die Schilddrüse, Thymus und andere Schlundspaltenderivate bei der Eidechse," von F. Maurer, *Morphol. Jahrbuch*, Bd. xxvii. p. 119, 1899.

[2] " Ueber den Bau und die Entwicklung der sog. Carotis drüse," von A. Kohn, *Archiv f. Mikr. Anat.*, Bd. lvi. p. 81, 1900.

do with excretory organs. The carotid gland is, according to him, the foremost of the suprarenal masses in the Elasmobranchs, viz., the so-called axillary heart.

In my opinion, nests of sympathetic ganglion cells necessarily mean the supply of efferent fibres to some organ, for all such ganglia are efferent, and also, if they are found in the organ, would have been taken in by the blood-vessels supplying the organ, so that, as already stated, Aichel's statement of the origin of the suprarenals in the Elasmobranchs seems to me much more likely than a derivation from nerve cells. If, then, it prove that Aichel is right as to the origin of the suprarenals, and Kohn is right in classifying the carotid gland with the suprarenals, then Maurer's statements would bring the para-thyroids, thymus, etc. into line with the adrenals, and suggest that they represented the segmented glandular excretory organs of the branchial region, into which, just as in the interrenals of Elasmobranchs, or the cortical part of the adrenals of the higher vertebrates, there has been no invasion of sympathetic ganglion cells.

Wheeler[1] makes a most suggestive remark in his paper on Petromyzon: he thinks he has obtained evidence of serial homologues of the pronephric tubules in the branchial region of Ammocœtes, but has not been able up to the present to follow them out.

If what he thinks to be serial homologues of the pronephric tubules in the branchial region should prove to be the origin of the thymus glands of Schaffer, then v. Wijhe's suggestion that the thymus represents the excretory organs of the branchial region would gain enormously in probability. Until some such further investigation has been undertaken, I can only say that it seems to me most likely that the thymus, etc. represent the lymphatic branchial glands of the Crustacea, and therefore re-present the missing coxal glands of the branchial region.

This, however, is not all, for the appendages of the mesosomatic region, as I have shown, do not all bear branchiæ; the foremost or opercular appendage carries the thyroid gland, again the basal part of the appendage is all that is left, the thyroid gland is in position a coxal gland. It ought therefore to represent

[1] *Op. cit.*, p. 22

the coxal gland of this appendage, just as the thymus, tonsils, etc. represent the coxal glands of the rest of the mesosomatic appendages. In the thyroid gland we again see a ductless gland of immense importance to the economy, not a useless organ, but, like the other modified coxal glands, impossible to remove without far-reaching vital consequences. Such gland, on the theory,[1] was in the arthropod a part of the external genital ducts which opened on the basal joint of the operculum.. What, then, is the opinion of morphologists as to the meaning of these external genital ducts ?

In a note to Gulland's paper[2] on the coxal glands of Limulus, Lankester states[3] that the conversion of an externally opening tubular gland (coxal gland) into a ductless gland is the same kind of thing as the history of the development of the suprarenal from a modified portion of mesonephros, as given by Weldon. Further, that in other arthropods with glands of a tubular character opening to the exterior at the base of the appendages we also have coxal nephridia, such as the shell glands of the Entomostraca, green glands of Crustacea (antennary coxal gland); and further on[4] he writes, "when once the notion is admitted that ducts opening at the base of limbs in the Arthropoda are possibly and even probably modified nephridia, we immediately conceive the hypothesis that the genital ducts of the Arthropoda are modi-- fied nephridia."

So also Korschelt and Heider,[5] in their general summing up on the Arthropoda, say :—

" In Peripatus, where the nephridia appear, as in the Annelida,. in all the trunk segments, a considerable portion of the primitive segments is directly utilised for the formation of the nephridia. In the other groups, the whole question of the rise of the organs known as nephridia is still undecided, but it may be mentioned as very probable that the salivary and anal glands of Peripatus,. the antennal and shell glands of the Crustacea, the coxal glands of Limulus and the Arachnida, as well as the efferent genital

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[1] Part IV. of this series of papers, *This Journal*, vol. xxxiii. p. 638.

[2] "Evidence in favour of the view that the coxal gland of Limulus and of other Arachnids is a modified nephridium," by G. Gulland, *Q. J. Micr. Sci.*, vol. xxv. p. 511, 1885.

[3] *Op. cit.*, p. 515.   [4] *Ibid.*, p. 516.

[5] *Text-book of Embryology,—Invertebrates*, part iii. p. 423.

ducts, are derived from nephridia, and in any case are mesodermal in origin."

The necessary corollary to this exceedingly probable argument is that glandular structures such as the uterine glands of the scorpion already described,[1] which are found in connection with these terminal genital ducts, may be classed as modified nephridial glands, and that therefore the thyroid gland of Ammocœtes, which, on the theory of these papers, arose in connection with the opercular genital ducts of the Palæostracan ancestor, represents the coxal glands of this fused pair of appendages. Such a gland, although its function in connection with the genital organs had long disappeared, still, in virtue of its original excretory function, persisted, and even in the higher vertebrates, after it had lost all semblance of its former structure and become a ductless gland of an apparently rudimentary nature, still, by its excretory function, demonstrates its vital importance even to the highest vertebrate.

By this simple explanation we see how all these hitherto mysterious ductless glands, pituitary, thymus, tonsils, thyroid, are all accounted for, are all members of a common stock—coxal glands—which originally, as in Peripatus, excreted at the base of the prosomatic and mesosomatic appendages, all retained because of the importance of the excretory function, although ductless, owing to the modification of their original appendages.

Finally, there is yet another organ in the vertebrate which follows the same law of the conversion of an excretory organ into a lymphatic organ when its connection with the exterior is obliterated, and that is the vertebrate body cavity itself. According to the scheme here put forth, the body cavity of the vertebrate arose by the fusion of a ventral prolongation of the original nephrocœle on each side ; prolongations which accompanied the formation of the new ventral midgut, and by their fusion formed originally a pair of cavities along the whole length of the abdomen, being separated from each other by the ventral mesentery of the gut. Subsequently, by the ventral fusion of these two cavities, the body cavity of the adult vertebrate was formed.

This is simply a statement of the known method of formation

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[1] Part IV. of this series of papers, *This Journal*, vol. xxxiii. p. 654.

of the body cavity in the embryo; and its phylogenetic explanation is, that the body cavity of the vertebrate must be looked upon as a ventral prolongation of the original ancestral body cavity.   Embryology clearly teaches that the original body cavity or somite was confined to the region of the notochord and central nervous system, and there, just as in Peripatus, was divisible into a dorsal part, giving origin to the myocœle, and a ventral part, forming the nephrocœle.   From this original nephrocœle are formed the pronephric excretory organs, the mesonephric excretory organs, and the body cavity.

That the vertebrate body cavity was originally a nephrocœle is generally accepted, and its excretory function is shown by the fact that it communicates with the exterior in all the lower vertebrates, either through abdominal pores or by way of nephridial funnels.   Bles[1] has shown how largely these two methods of communicating with the exterior mutually exclude each other.   In the higher vertebrates both channels become closed, except in the case of the Fallopian tubes, and thus, so to speak, the body cavity becomes a ductless gland, still, however, with an excretory function, but now, as in all other cases, forming a part of the lymphatic rather than of the true excretory system.

CONCLUSIONS.

The consideration of the formation of the vertebrate cranial region, as set forth in the previous ten parts of this series of papers, indicates that the ancestor of the vertebrates was not an arachnid purely or a crustacean purely, but possessed partly crustacean and partly arachnid characters.   In order to express this conclusion, I have used the term Protostraca, invented by Korschelt and Heider, to indicate a primitive arthropod group from which both arachnids and crustaceans may be supposed to have arisen, and have therefore stated that the vertebrate did not arise directly from the annelids, but from the Protostraca. Such an origin signifies that the origin of the excretory organs

[1] "On the openings in the wall of the body cavity of Vertebrates," by E. J. Bles, *Proc. Roy. Soc.*, vol. 62, p. 232, 1897.

of the vertebrate must not be looked for in the segmental organs of the annelid, but rather in such modified annelid organs as would naturally exist in a primitive arthropod group. The nature of such organs may be inferred owing to the fortunate circumstance that so primitive an arthropod as Peripatus still exists, and we may conclude that the protostracan ancestor possessed in every segment a pair of appendages and a pair of cœlomic cavities which extended into the base of these appendages. The ventral portion of these cœlomic cavities separated off from the dorsal and formed a nephrocœle, giving origin to a segmental excretory organ, which, seeing that its end vesicle was in the base of the appendage, and seeing also the nature of the known arachnid and crustacean excretory organs, may fitly be termed a coxal gland. This, then, is the working hypothesis to explain the difficulties connected with the origin of the pronephros and mesonephros—that the original segmental organs were coxal glands, and therefore indicated the presence of appendages. This hypothesis leads to the following conclusions :—

1. The coxal glands belonging to the post-branchial appendages of the invertebrate ancestor are represented by the pronephric tubules, and existed over the whole metasomatic region.

2. Such glands discharged into a common duct—the pronephric duct—which opened into the cloacal region, either in the protostracan stage, when the metasomatic appendages were still in existence, just as the coxal glands of the prosomatic region in Limulus discharge into a common duct, or else the pronephric duct was formed when the appendages were obliterated.

3. The metasomatic appendages disappeared owing to their enclosure by pleural folds, which, meeting in the mid-ventral line, not only caused the obliteration of the appendages, and gave a smooth fish-like body surface to the animal, but also caused the formation of an atrial cavity.

4. Into these pleural folds the dorsal longitudinal muscles of the body extended, and ultimately reached to the ventral surface, thus forming the somatic muscles of the vertebrate body.

5. When the pleural folds had met in the mid-ventral line the animal had become a vertebrate, and was dependent for its locomotion on the movements of these somatic muscles, and not on the movements of appendages. Consequently, elongation of

the trunk region took place, for the purpose of increasing mobility, by the formation of new metameres.

6. Each of such metameres possessed its own segmental excretory organ, formed in the same way as the previous pronephric organs, but, as there were no appendages in these new formed segments, the excretory organs took on the characters of a mesonephros, not of a pronephros, and opened into the pronephric duct, because the direct way to the exterior was blocked by the enveloping pleural folds.

7. The group of annelids from which the protostracan ancestor of the vertebrates arose was the highest annelidan group, viz., the Polychæta, as shown by the nature of the excretory organs in Amphioxus.

8. The coxal glands of the protostracan ancestor existed on all the segments, and were therefore divisible into three groups, prosomatic, mesosomatic, and metasomatic; these three groups of coxal glands still exist in the vertebrate as ductless glands.

9. The prosomatic coxal glands form the pituitary body.

10. The mesosomatic coxal glands form the thymus, thyroid, parathyroids, tonsils, etc.

11. The metasomatic coxal glands form the adrenals.

12. The procœlom of the vertebrate is the procœlom of the protostracan ancestor, which splits into a dorsal part, the myocœle, and a ventral part, the nephrocœle. This latter part not only forms the pronephros and mesonephros, but also by a ventral extension gives origin to the walls of the vertebrate body cavity or metacœle.

13. This ventral extension of the original nephrocœle at first excreted to the exterior through abdominal pores or through peritoneal funnels. When such paths to the exterior became closed, it also became a ductless gland, belonging to the lymphatic system.

CAMBRIDGE, *May* 1902.

Journal of Anatomy and Physiology.

ON THE DEVELOPMENT AND HOMOLOGY OF THE MAMMALIAN CEREBELLAR FISSURES.[1] By O. CHARNOCK BRADLEY, M.B., *Professor of Anatomy, Royal Veterinary College, Edinburgh.* (PLATES XVII.–XXIII.)

PART II.—PIG.

40 *days embryo*, 52 *mm. long* (figs. 54, 55 and 56).—At this stage the cerebellum of the pig embryo bears a certain likeness to that of the rabbit on the 20th day of gestation. No fissures are visible to the naked eye, but when sections are made and microscopically examined there is noticed a somewhat thin lip-like plate projecting from the lower posterior corner of the section of the cerebellar lamina (fig. 56). This is comparable in every respect to the same feature in the rabbit's brain on the 20th day, and there develops a homologous lobe in connection with it.

44 *days embryo*, 64 *mm. long* (figs. 57, 58 and 59).—Development has proceeded rapidly during the interval between the last stage and the present. A naked-eye examination shows a sufficiently clear distinction between the future vermis and hemispheres. There is also visible on the anterior slope a fissure (II.) of considerable length (fig. 58). Microscopic sagittal sections show fissure IV. as before, and fissure II. of some depth. There are also possibly faint indications of two other fissures in that part of the vermis lying between II. and IV. There is as yet no trace of a separation of a paraflocculus from the hemisphere.

48 *days embryo*, 80 *mm. long* (figs. 60, 61 and 62).—Develop-

ment has again progressed rapidly; indeed, it is something of a misfortune that a stage intermediate between 44 and 48 days could not be obtained. But though this is a misfortune, it is not one which offers any insuperable difficulty in the solution of the problem before us.

An examination of a 48 days cerebellum reveals a fissure (II.) which is prolonged for some distance into the hemisphere. Below it the two other fissures are faintly marked. These develop into fissures I. and c. On the posterior slope there are two faint fissures in the vermis. Subsequent development shows that these become fissures III. and d. In the hemisphere there is an indication of a fissure, which, growing inwards from the lateral part of this portion of the cerebellum, ultimately demarcates the paraflocculus. Another faint foreshadowing of a fissure is also seen indenting the margin of the hemisphere anterior to the one just mentioned. This latter, growing inwards, ultimately forms part of fissure a (fig. 60, a).

Microscopic sections afford additional evidence as to the actuality of the faint depressions seen with the naked eye (fig. 62). They also show that a number of fissures are about to complicate that portion of lobe A which lies below fissure c (lobule A_1). Lobe E has increased in volume, and is now, in consequence, sharply defined from the posterior medullary velum. A flocculus is becoming evident, and its development from the boundary of the lateral recess is clearly indicated. Its boundaries are not as yet rigidly set down, but it reveals itself as a thickening and bulging in the region in which, in the future, it is to become conspicuous (fig. 61).

Embryo, 86 mm. long.—In the cerebellum of an embryo of 86 mm. in length (of which the age is not certainly known, but is estimated at about 50 days) the anterior surface is quite richly fissured. Fissure II. now reaches the extreme margin of the hemisphere, and fissure I. almost does so. On the posterior slope, fissure a runs completely across the cerebellum, but is shallow at the junction of vermis and hemisphere. Fissure III. crosses the vermis and invades the groove between it and the hemisphere. The fissure which is about to cut off the paraflocculus is deep, and is growing inwards towards fissure III. of the vermis, with which it finally becomes continuous.

Fissure d is, if anything, rather longer than fissure III. The paraflocculus forms a distinct projection, and is now clearly separated from the flocculus. Sections show that lobe B is becoming divided by a shallow transverse fissure.

51 *days embryo*, 88 *mm. long* (figs. 63, 64 and 65).—The difference between this and the above stage is only one of depth of fissures.

55 *days embryo*, 100 *mm. long* (fig. 66).—To the naked eye the fissures have obviously deepened since the 51st day, but no new ones can be made out. Sections, however, show that a fissure, b, has begun to invade that part of lobe C which is in the vermis. It seems likely that this fissure first made its appearance, on the anterior slope of the hemisphere, about the 48th day (fig. 61), and that the two parts gradually grew together in the vermis. It is interesting to notice at what an early period fissure a came into existence, and how comparatively late fissure b is in making its appearance in the vermis. This should be compared with the constancy of the former fissure in the cerebella of the type of the rabbit, and the inconstancy or difficulty of determination of fissure b in the cerebella of the same order of complexity.

The fissures in lobule A_1 are now of considerable depth. Lobule A_2 retains its comparatively small size. Lobe B is larger, and contains a moderately deep fissure, which is the forerunner of a like feature in the adult brain.

59 *days embryo*, 118 *mm. long* (figs. 67, 68 and 69).—As in the rabbit, the anterior part of the pig's cerebellum has advanced more rapidly than the posterior part during the earlier stages of development. By the 59th day the anterior surface is bearing a strong resemblance to the adult condition, but the posterior part is still comparatively simple. Fissure b is now of some depth and can readily be recognised by the unaided eye. Fissure a has gained considerably in depth. Fissure III. has become continuous with the lateral fissures, which, making an early appearance, first indicated the limits of the paraflocculus.

Fissure d is of great lateral extent, being indeed the longest fissure of the cerebellum at this stage (with the possible doubtful exception of fissure II., which has a curved course). Fissure d, it should be noted, is growing forwards into the

paraflocculus, which is, by it, being divided into an upper and a lower part, connected together in front (fig. 67). It is desired to emphasise the fact that there is a strong, well marked connection between lobe D and the paraflocculus. This connection at this stage is not confined to the part of lobe D above fissure *d* (lobule D_1), but belongs to the entire lobe. Nothing could show more clearly that the paraflocculus and lobe D are parts of one and the same morphologic unit. This point is illustrated much better in the pig than it was in the rabbit.

The paraflocculus has enlarged, and its anterior surface shows signs of foliation (fig. 68).

65 *days embryo*, 132 *mm. long* (figs. 70, 71, 72, 73 and 74).— The anterior surface has now very closely approached the adult condition, both in its external appearance and also in those features which can only be adequately appreciated by means of sagittal sections.

Fissure II. is of great depth, its lowest part being not far removed from the summit of the roof of the 4th ventricle (fig. 74). Lobe B shows definite evidence of its future bipartite condition. Lobule A_1 has now lost its former arrangement of indefinitely arranged folia, and has collected them into three sub-lobules such as are found in the adult brain. Fissure *b* is now of some depth, and fissure *a* makes an important landmark on the posterior slope. Fissure *d* is deeper than fissure III., and both parts of lobe D are becoming foliated (fig. 74). Lobe E remains relatively small and simple, but is now separated from the posterior medullary velum by a conspicuous fissure.

The paraflocculus is now divided into two parts, both of which are now foliated. The whole lobule now closely resembles the same lobule in the adult squirrel. The division into two parts has obviously been brought about by an extension in a forward direction of fissure *d*. This extension was beginning in the previous stage. The upper part of the paraflocculus is connected with lobule D_1 by a rounded non-foliated ridge. The connection between lobule D_2 and the lower half of the paraflocculus has almost become obliterated, but it should be kept in mind that such a connection did at

one time exist. The flocculus is small and, to the naked eye, not yet provided with folia. On examining microscopic sections, however, slight fissures are found to exist.

70 *days embryo*, 150 *mm. long* (fig. 75).—Except in richness of foliation, no marked change has occurred in that part of the cerebellum which is anterior to fissure II. The posterior portion of the organ, however, has now entered into a more active phase of development, and is rapidly assuming the adult appearance. That part of lobe C which is anterior to fissure *a* (lobules C_1 and C_2) has grown considerably in a lateral direction. Further, the vermis portion has also grown so much in an antero-posterior direction that it can no longer be accommodated in the strict mesial plane, but has become distorted by being thrust over to one side. Fissure *b* is now a very important feature. It extends all the way across the cerebellum. Lobule C_3 has also altered considerably in appearance. It no longer forms a band of practically uniform width, running from one margin of the cerebellum to the other. It now fails to extend as far laterally as the more anterior part of lobe C. Its vermis portion has increased in volume in a sagittal direction, and, like that part of the vermis immediately in front of it, is now distorted by being pushed to one side. The hemisphere portions, too, have enlarged in a sagittal direction, and are now in the form of rounded masses, connected with the vermis by a comparatively narrow isthmus. This lobule has therefore come to resemble that of the squirrel.

The two parts of lobe D have also enlarged, and their folia are more numerous. The connection between lobule D_1 and the corresponding part of the paraflocculus is still smooth. Lobe E remains small, and to the naked eye appears to have no connection with the flocculus beyond that established by means of the posterior medullary velum. But microscopic sections show that there is still a low smooth ridge running between the two structures.

The paraflocculus has not increased much in size, and, because of the lateral expansion of lobe C, is now not so prominent a feature on the lateral surface of the hemisphere. The flocculus is still small, and to the naked eye smooth.

Embryo, 165 *mm. long, age unknown* (figs. 76, 77, 78, 79

and 80).—This is the last embryonic stage which it is necessary
to examine, as it brings us within a short distance of the
condition of the adult cerebellum.   Lobule A_1 is now certainly
composed of three sub-lobules, the uppermost of which has
beyond doubt an extension into the hemisphere.   One single
small folium still adheres to the anterior medullary velum,
and therefore may possibly be looked upon as an attenuated
example of a lingula.   Lobule A_2 is relatively small, and has a
rather shallow fissure dividing it into two parts.   Fissure II.
begins on the dorsal surface of the vermis; curving forwards
at the lateral boundary of the vermis, it runs obliquely down
the anterior surface.   Lobe B is divided into upper and lower
portions by a fairly deep fissure, whose advent has been noted
in earlier stages.   Lobe C has again made great advances.   So
much is this the case that lobule C_2 is very considerably
distorted.   Lobule C_3 is now clearly divided into three parts—
one in the vermis and one in each hemisphere—connected by
narrow bands.   The connection between lobule D_1 and the
upper part of the paraflocculus is becoming slightly marked
by fissures, and has become in part hidden by the posterior
extremity of lobe C.

The paraflocculus is now quite complicated, from the presence
of numerous folia; but there is no difficulty in recognising its
constitution as two tiers.   The flocculus is now foliated.

Adult cerebellum (figs. 81, 82, 83 and 84).—Having traced
the development of the fissures and lobes up to an advanced
stage, it does not seem necessary to give an additional detailed
description of the adult organ.   It will suffice to briefly indicate
the changes which have occurred since the 165 mm. stage.

The cerebellum anterior to fissure II. has not undergone any
radical change.   It has taken additional folia upon itself, but
that is all.   In the posterior part of the cerebellum more
decided changes have occurred.   Fissure *b* is now very distinct
crossing vermis and hemisphere, and reaching the border of the
latter.   A further displacement of the vermis portion of lobe
C has taken place, so that in the adult brain fissure *a* is
decidedly oblique.   The connections between the vermis and
hemisphere portions of lobule C_3 have become very much reduced.
The upper part of lobe D has shared in the general distortion of

this region of the vermis.   Its connection with the paraflocculus now consists of a transversely foliated ridge (fig. 83).   Lobule D_2 has merely increased in size and become more thickly foliated. Lobe E remains very small and inconspicuous (fig. 84).

In many cerebella the paraflocculus has become a somewhat jumbled collection of folia, but in most brains it has retained a closer resemblance to its earlier condition.   There is usually little difficulty in tracing its two-tiered character, but it appears as though the lower tier had been turned forwards at its posterior end.   The flocculus in the adult is in the form of a row of vertically placed folia, and runs in an antero-posterior direction, immediately below the paraflocculus.   Its extremities only are visible when the cerebellum is looked at from before or from behind.

Having now learnt the characters of the fissures and lobes in the pig, we are in a position to examine those cerebella which are constructed after a similar plan.

Mustela furo (figs. 85, 86, 87 and 88).—In this animal is a good example of the backward retreat that fissure II. makes in some of the more complex cerebella.   The vermis is about equally voluminous in front of and behind this fissure, this being the result of an increase in the number of lobules in the more anterior section of the vermis.

Lobe A is divided into two slightly unequal parts by a fissure, *c*, which is almost entirely visible when the cerebellum is looked at from the front, and which reaches the margin of the hemisphere.   Lobule A_1 is divided into two parts, each carrying two or three folia.   Lobule A_2 is also divided into two portions, but the fissure is not so deep as that in lobule A_1.   Lobe B is cut by a curved fissure which almost reaches its lateral boundaries. It will be seen that lobes A and B are very similar to the corresponding lobes in the pig, except that the lower component of A is divided into two instead of three sub-lobules.

Lobe C forms a very considerable constituent of the hemisphere.   It has fissures *a* and *b*, but the lobules in the vermis between *a* and *b* and *a* and III. are comparatively simple; *i.e.* they are not developed to such an extent that their accommodation necessitates distortion of the vermis.   The connection between vermis and hemisphere segments of lobule C_3 is very

narrow, as in the pig, and partly or wholly concealed. Lobes D and E are confined to the vermis; and D is divided into two lobules by a fissure, d.

The paraflocculus is arranged in the form of two tiers of folia joined together anteriorly. From the lower tier a lobulus petrosus projects for some distance. The connection between paraflocculus and lobe D cannot be made out in the adult. It is somewhat difficult to satisfactorily distinguish a flocculus, but it is apparently present, and visible when the cerebellum is viewed from the side or from behind.

Mustela erminea and *M. vulgaris* have both been examined, but they so closely resemble *M. furo* that no further description is necessary.

Meles taxus (figs. 89, 90, 91 and 92).—As compared with lobe B, lobe A is smaller in the badger than it is in the pig. Only a comparatively small portion of it is visible on the anterior surface of the cerebellum. Lobule A_2 is also small. Below fissure c there are two groups of folia, that group lying more inferiorly being further partially divided.

Lobe B is large, and divided by a deep fissure into upper and lower lobules, each of which is again somewhat deeply indented by a fissure (fig. 92).

In lobe C, fissure b extends to the border of the hemisphere, as it does in the pig (fig. 90). Lobule C_2 consists of a vermis portion, whose folia—unlike those of the pig—run transversely; and a hemisphere part, considerably removed from the vermis, because of the large development of those parts of lobule C_3 which belong to the hemisphere. The three segments of lobule C_3 are very unequal in size, the hemisphere portions being very extensive. There is practically no distortion of lobule C_3 in the vermis (fig. 91). Lobes D and E call for no special remark. The double character of the paraflocculus is very evident, the two portions being arranged in an oblique plane, and very clearly continuous in front (figs. 89 and 90). The connection between paraflocculus and vermis is very difficult to establish. In the brain examined, a very prominent lobulus petrosus was present on the right side, and was received into a fossa formed by the temporal bone. On the left side the corresponding lobule was curved forwards underneath the lower part of the

paraflocculus (fig. 89). The question arises as to the possibility of the lobulus petrosus always representing the posterior extremity of the lower portion of the paraflocculus. This may be the case. If we accept this as being a true interpretation of the facts, then we should consider that, as the paraflocculus increases in size in different animals, it tends to press forwards, since the lobulus petrosus is often found in cerebella having small paraflocculi.

The flocculus consists of a single folium lying between the lateral recess of the ventricle and the most posterior part of the paraflocculus.

Canis familiaris (figs. 93, 94, 95 and 96).—The anterior part of the cerebellum of the dog does not differ very materially in the arrangement of its fissures and the disposition of its lobes from the corresponding part of the badger's cerebellum. In lobes C and D, however, there are differences of sufficient magnitude to warrant mention. Fissure *b* is present in a position very similar to that of the badger. It can readily be followed across the vermis and hemisphere to the border of the latter, running almost parallel to fissure II. Lobule C_2 has a very considerably distorted vermis portion, and its hemisphere dependencies show several fissures of some depth, which give the impression that it consists of several distinct sub-lobules. The central segment of lobule C_3 is also much twisted, and on superficial examination appears to have no connection with those vertically elongated masses which form its hemisphere segments. On opening up the groove between vermis and hemisphere, however, the connection can be distinguished. The displacement and sinuousness of the vermis in lobules C_2 and C_3 only appears after birth. In a new-born dog the vermis is perfectly straight and its folia entirely transverse.

Lobule D is connected to the upper part of the paraflocculus by a low white ridge, which can only be discovered by removing the lowest and most posterior part of lobe C. The rest of lobe D and lobe E call for no remark.

The paraflocculus is relatively larger than that of the badger, to which it bears a close resemblance in the manner in which its two tiers are arranged. It has not, however, a lobulus petrosus; or, at any rate, there is not more than the merest

attempt at the formation of one, this occurring at the posterior end of the lower tier, and being only occasionally present. The flocculus is small and consists of a few folia, placed, under cover of the paraflocculus, at the most anterior limit of the lateral recess of the ventricle (fig. 95).

Canis vulpes (figs. 97, 98 and 99).—The general shape of the cerebellum of the fox is very different from that found in the dog. The fox's cerebellum has a greater vertical height in comparison with its antero-posterior diameter. Its anterior surface is depressed for the reception of the corpora quadrigemina, and its posterior surface is also concave from above downwards. The posterior concavity is rendered all the more obvious because of the backward projection of lobe D over the medulla. This projection is confined to lobule D_2, and is so great that this lobule can be seen very distinctly when the cerebellum is viewed from above. These differences being recognised, the cerebellum of the fox otherwise resembles that of the dog. The only points to which it seems necessary to draw attention are two, as follows : The vermis in the region of lobules C_2 and C_3 is possibly a little shorter in an antero-posterior direction, and somewhat less distorted in form. The lower part of the paraflocculus carries a definite lobulus petrosus (figs. 97 and 98).

The flocculus is small in the fox, and only just visible from behind (fig. 98).

Felis domestica (figs. 100, 101 and 102).—In the domestic cat the anterior part of the cerebellum is so similar to the same portion in the dog, both as regards its superficial characters and also its appearance in sections, that no detailed description is needed. The most important features are those presented by the organ when viewed from behind. Several cerebella of the cat have been examined, and in all a very striking character is the extreme to which the distortion of the central portions of lobules C_2 and C_3 is carried (figs. 100 and 101). In the brain from which the figures were made this distortion is very marked, possibly more so than is the case in the average cerebellum; but they serve to show to what lengths this twisting of the vermis may go. It will be observed that lobules C_2 and C_3 are arranged in the form of an S-shaped curve, the bends of

which are very abrupt. This curvature of the vermis is continued into lobe D, but here its bends are not so sudden (fig. 101). There can be little doubt that this exaggerated displacement of the vermis is to be interpreted as meaning that, in the cat, lobes C and D are relatively more developed (so far as those parts of them which belong to the vermis are concerned) than is the case in the other mammals examined. The lateral parts of lobule C_3 are relatively smaller in the cat than in the dog, badger, or fox (fig. 101). They do not extend so far downwards as to blot out the connection between paraflocculus and the vermis. This connection is in the form of one or two folia, resting upon the medulla below, and in contact with the lowest part of lobule C_3 above.

The paraflocculus resembles that structure in the dog. There is considerable difficulty in distinguishing a flocculus with any degree of certainty in the adult animal. That it is present is undoubted from the observations made by Stroud on its development. But its clear definition in the embryo appears to become obscured at a later date.

Goat and Sheep (figs. 103, 104 and 105).—In many respects the cerebellum of ungulates departs, in the way of details, from the plan found in those carnivora just described.

When viewed from the front, the cerebella of the goat and sheep show fissures *c*, I., II. and *b* very distinctly (fig. 103), all of these reaching the margins of the hemisphere. Fissure *c* crosses the vermis almost perfectly transversely. Lobule A_1 has only a very imperfectly developed hemisphere portion; indeed it is doubtful if the hemispheres can be considered to extend into this region. Fissure I., possibly a little shallower than *c*, has a curved direction. Fissure II. is very acutely curved, as in the dog. Lobule A_2 and lobe B are almost entirely confined to the vermis, their lateral prolongations being very small. Indeed, in this region it is difficult to set definite bounds between the vermis and the hemispheres. There is some amount of lateral displacement, with consequent curvature, in the vermis in lobules C_2 and C_3, but this is not greater in amount than that found in the dog.

In the sheep and goat, and in ungulates generally, the lateral divisions of lobule C_3 are not nearly so large as they are in the

carnivora. In the carnivora their uppermost ends are commonly visible, either on one or both sides, when the cerebellum is regarded from the front. This has never been found to obtain in those ungulates which have been examined for the purposes of this research. Again, these lobules do not reach so far down as to touch the medulla, other than in exceptional cases. The result of this vertical abbreviation is to allow of the connection of the paraflocculus to be traced directly to the vermis, as is the case in the simpler forms of cerebellum (fig. 104). As we have seen, this connection is easily made out in the adult pig. In the sheep and goat, however, it is not quite so evident on a superficial examination; it is necessary to open up the groove between vermis and hemisphere.

The form of lobule D_1 is somewhat peculiar in both the sheep and goat (fig. 104). It has a central, well developed portion in the vermis, and smaller offshoots reaching into the hemispheres, a constriction of greater or less tenuity intervening.

Lobe E is of larger size than in the pig and the carnivora. The paraflocculus and flocculus resemble those parts of the cerebellum of the pig.

Bos taurus (fig. 106).—In the cerebellum of the cow, although the same lines are followed as in the sheep and goat, the arrangement of fissures appears at first sight to be very complicated. This remark applies only to the superior and posterior views, as lobes A and B and lobule C_1 are almost identical in form with those parts in the average carnivore or ungulate brain. It may be added that it is impossible to make out any hemisphere in lobe A. Even in lobe B the hemisphere is very attenuated.

On closely examining the posterior part of the cerebellum, it is found that the complexity is more apparent than real, and is due to a distortion which rivals that of the cat's vermis. Apart from this disturbance of form, there is little to which special attention need be directed. It may be mentioned, however, that the lateral parts of lobule C_3 commonly extend farther in a downward direction than obtains in the sheep and goat, this extension bringing them almost or quite in contact with the medulla. Not infrequently lobe E is so large and projects so far backwards as to be visible as one or two folia on the posterior aspect of the cerebellum.

Equus caballus (figs. 107, 108 and 109).—A very striking feature in the horse's cerebellum is the comparatively posterior position of fissure II. Fissures *c*, I., II. and *b* are distinct and deep. Fissure *c* is of very considerable depth, and fissure I. is almost as deep as fissure II. (fig. 109). It should be noted—as distinguishing the cerebellum of the horse from that of the sheep and goat, and especially from that of the cow—that lobe A is certainly, though not very strongly, continued into the hemisphere.

The posterior part of the horse's cerebellum shows one or two points of interest and importance. As in the ungulates already mentioned, the lateral parts of lobule C_3 are small as compared with the carnivora. In the horse their connections with the vermis are not difficult to follow. There is, further, no difficulty in making out the connecting link between lobule D_1 and the paraflocculus (fig. 108).

In some specimens lobule D_2 is continued into the hemisphere for a short distance, but this continuation has only once been found on both sides in the same brain. Its presence, though inconstant, is interesting, as being apparently the remains of that undoubted connection which we have seen to exist between lobule D_2 and the lower part of the paraflocculus during the embryonic life of the pig. In the majority of animals all trace of this primitive unity is lost as the brain grows into its adult form; but in some, possibly in man, evidences remain.

Lobule E is, if anything, smaller in the horse than it is in the sheep, goat and cow. The paraflocculus shows its two-tier character more clearly than in the other ungulates examined, in this respect resembling the paraflocculus of the carnivora. It should be remembered that in ungulates generally the lower tier shows a tendency to curve forwards at its posterior end. This is so well marked in the horse that there are practically three tiers produced. In an earlier part of this paper the suggestion has been thrown out that possibly the lobulus petrosus of the rabbit, etc. represents only the posterior extremity of the lower part of the paraflocculus of more complex cerebella. It may be asked, further, whether in those animals like the horse, in which the paraflocculus turns forwards at its posterior end, this

recurved extremity may not be equivalent to a lobulus petrosus, unenclosed in a special fossa of bone. The supposition that this may be so is strengthened when the condition found in the badger is taken into account. In the cerebellum of *Meles taxus*, of which a description has already been given, on one side a lobulus petrosus was found; but on the other side the corresponding part of the paraflocculus was turned forwards underneath the lower tier.

The flocculus is usually easily distinguished in the horse, and is visible from the side and from behind. In some specimens a distinct white ridge, independent of the posterior medullary velum, passes from the flocculus to lobe E of the vermis. This ridge is indicated on the left side of fig. 108. It has not been met with elsewhere than in the horse—possibly because an insufficient number of cerebella have been examined—but its occurrence in this animal is of importance, as showing evidence, in the adult, of the embryonic unity of the structures between which it passes.

Equus asinus.—The cerebellum of the donkey is so like that of the horse in all but the merest details that an extended description is not necessary. It may perhaps be well to say that lobule C_2 in the hemisphere carries several fairly deep fissures, whose presence give the surface a complex appearance. Lobule D_1 shows the tendency, remarked in the sheep and goat, to extend into the hemispheres in the form of lateral append-ages. The connection of this lobule with the paraflocculus is not so superficially evident as it is in the horse. The flocculus of the donkey has a greater antero-posterior extent than is the case in the horse.

In the foregoing pages the steps by which the fissures, and consequent lobes and lobules, of the cerebellum came into existence have been traced in two mammals. It has also been sought to discover the simplest form of mammalian cerebellum, and this having been done, to endeavour to recognise, in the complex as well as in the simpler forms, a likeness to this elementary pattern. Apparently the cerebellum in which the fissures are fewest and the lobes smoothest belongs to the shrew and the smaller bats. In the shrew there are four

fissures only; and of these only one (the second, *i.e.* II.) extends through both vermis and hemisphere. The remaining three do not belong to the hemisphere, being confined to the vermis or its immediate neighbourhood.

In following the development of the cerebellum of the rabbit, it was found that this five-lobed and four-fissured stage was reproduced. But in the adult rabbit the number of fissures is increased. In the development of the pig, it appears possible that the five-lobed condition may obtain in its simple form for a time, but it quickly gives place to a much greater complex of fissures.

In both rabbit and pig fissure IV. was the first to appear, and this in association with the Rautenlippe, which, continuing round the lateral recess of the ventricle, blends with the Rautenlippe of the medulla. The association of fissure IV. originally seems beyond doubt. But as development goes on it becomes more and more removed from the edge of the cerebellar lamina, because of the growth of lobe E and the flocculus.

In both rabbit and pig the second fissure to develop is fissure II., which has been recognised by several writers to be of paramount importance, and which is declared by both Stroud and Kuithan to be the first fissure visible in the developing cerebellum.

The next fissures, in point of time of appearance and importance as dividing lines of the cerebellum, are fissure III. and those demarcating the paraflocculus from the rest of the hemisphere. These three are in reality the three elements of one and the same fissure, which, becoming continuous, they ultimately form.

By the presence of the above mentioned fissures, the cerebellum becomes divided transversely (but not completely as yet) into four unequal portions. (1) A part anterior to fissure II.; this becoming itself divided later into lobes A and B by fissure I. (2) Lobe C, lying between fissure II. and fissure III., with its lateral elements. (3) Lobe D, to which the paraflocculus belongs. And (4) lobe E, of which the flocculus is an outlying dependency.

Fissure I.; separating lobes A and B, appears shortly after fissure III. in the rabbit, and somewhere about the same time in the pig. The other fissures, which are formed either at the same time

as some of the above (as in the pig), or at a somewhat later date (as in the rabbit), may be considered as of secondary importance, and have no representatives in the simplest type of mammalian cerebellum.

In those adult cerebella which have been examined, there is quite clearly a common pattern running through the whole series. But in many of them there are interwoven into this fundamental pattern subsidiary ornaments, which tend, in a measure at least, to obscure the simplicity of the cerebellum which has been taken as the starting-point. In all the cerebella the five fundamental lobes can be recognised, and their individual peculiarities and tendencies may be summarised as follows :—

Lobe A, in all but the very simplest forms, is divided into two unequal parts by fissure c. This fissure is wanting in the shrew and indefinite in the hedgehog, but is constant in all others. Lobule A_1 in the higher forms consists of three sub-lobules. In some there are apparently only two of these divisions. It is possible that this complexity of the lobule may be indicated even in the rabbit. Lobule A_2 is always smaller than lobule A_1, and is generally provided with a moderately deep fissure, whose precursor may possibly be shown in the rabbit.

In the higher forms lobe B is divided into two parts, each of which may be again divided. In the rabbit and hedgehog it carries two folia, separated by a moderately deep fissure.

Lobe C consists of three lobules, separated by fissures a and b. Of these two fissures a is held to be much the more important morphologically, because of its earlier appearance in the embryo and its more constant character in the adult. These two fissures apparently develop in a manner peculiarly their own. They both begin in the hemisphere, and grow towards the middle line.

Lobule C_3 must be considered as standing definitely apart from the rest of lobe C. Its differentiation is early, especially in the pig, and in all the adult animals described, from the squirrel upwards, its individuality is very strongly asserted.

Even in the rabbit there is an attempt at a division of lobe D, but this is not accomplished until the squirrel is reached.

In the higher forms the division is embryonic and early. In the pig, fissure *d* appears about the same time as fissures III. and I. Particular attention has been called to the development of fissure *d* because of its forward extension and invasion of the paraflocculus, which is, as a result, divided into two parts, as is the rest of lobe D to which it belongs. Subsequent development may obscure the continuity of the paraflocculus with lobule D_1, or, on the other hand, the connection may persist into adult life (*e.g.* in the horse). The connection of the paraflocculus with lobule D_2 is always lost in the adult, but there may remain slight traces, such as are found in the horse.

The embryonic continuity of lobe E and the flocculus, and their morphologic unity, have already been commented upon. This continuity early disappears, and there is usually no trace of it apart from the posterior medullary velum. But in the horse at least, as has been noted, some evidence may exist even in the adult.

The various fissures and lobes have been distinguished, up to this, by letters and figures only. It would have been easy to employ terms such as those used in human anatomy, but—as Oliver Wendell Holmes has expressed it—words, from occupying for a long time the same place in language, become 'polarized.' So, in order to trammel the mind as little as possible, it was thought better to avoid those terms which would call up certain fixed and long-rooted conceptions.

The purpose of keeping the judgment as unbiassed as possible being now served, the letters and figures may give place to terms such as are commonly employed. In order to do this, the notion of the plan of the mammalian cerebellum, which has been gained from the descriptions given herein, must be applied to the cerebellum of man. Using the technicalities as employed by Schäfer in *Quain's Anatomy*, the letters and figures may be transmuted as follows:

There can be little doubt that fissure II. corresponds to *sulcus preclivalis*, fissure III. to *sulcus postpyramidalis*, and fissure IV. to *sulcus postnodularis*. Fissures *a* and *b* correspond respectively to *sulci horizontalis magnus* and *postclivalis*, and fissure *d* is equivalent to *sulcus prepyramidalis*. That sulcus horizontalis magnus should not be employed, as is done in human anatomy,

to divide the cerebellum into two primary parts, is evident, and
has been pointed out and insisted upon by Stroud. The com-
parative method clearly shows that sulcus preclivalis (*furcal
sulcus* of Stroud) forms the real and fundamental dividing line.

In that part of the cerebellum which falls anterior to fissure
II. (sulcus preclivalis), difficulties arise in the use of human
anatomical terms. For *sulcus postcentralis* of the human
anatomist corresponds to fissure *c*; a fissure secondary both in
point of time of appearance in the embryo and in morphologic
value. In the current descriptions of the human brain, as
given in this country, no sulcus is mentioned as equivalent to
fissure I. The result is that the culmen of human anatomy
includes lobe B and lobule A_2. Lobule A_2 probably corresponds
to the "ascending part of the monticulus" of some German
writers (Flatau and Jacobsohn, for instance), but I am not
certain that the expression is used for lobule A_2 alone or
always.

The following table shows the parts in the human brain
corresponding to the various divisions of the mammalian cere-
bellum as described in this paper.

FISSURES.	LOBES.	
c. Sulcus postcentralis	Lobus centralis. A_1.	⎱ A.
	A_2.	
I. (Not named by Schäfer)	Lobus culminis	
II. Sulcus preclivalis		⎱ B.
b. Sulcus postclivalis	Lobus clivi. C_1.	
	Lobus cacuminis. C_2.	⎱ C.
a. Sulcus horizontalis magnus		
	Lobus tuberis. C_3.	
III. Sulcus postpyramidalis	Lobus pyramidis. D_1.	
d. Sulcus prepyramidalis		⎱ D.
	Lobus uvulæ. D_2.	
IV. Sulcus postnodularis		
	Lobus noduli.	⎱ E.

It will be observed that I have only examined the cerebella
of placental mammals. Lack of suitable material has precluded
a first-hand investigation of Monotremes and Marsupials. But,

judging from the descriptions and figures given by Ziehen (7), it is clear that the scheme, as elaborated in the foregoing pages, will apply to Marsupials at least. These mammals evidently fall into the group of animals in which the cerebellum follows the simpler type. Whether Monotremes also can be included in this group is not so obvious from the descriptions available. It seems not unlikely that their cerebella belong to a group separate from the rest of the mammalia.

In carrying out the work of this investigation, so much assistance, in the form of material, has been afforded by so many persons, that it is impossible to make suitable acknowledgment without going to considerable length. Let it suffice to say, that my debt of gratitude is not to be computed from the extent of the avowal here made. Much of the microscopic work has been done in the Physiological Laboratory of the University of Edinburgh, where, through the courtesy of Professor Schäfer and his assistants, every facility that could be wished for has been afforded.

REFERENCE.

(7) ZIEHEN, TH., "Das Centralnervensystem der Monotremen und Marsupialier. Thiel I. Macroscopische Anatomie," *Jenai'sche Denkschriften*, vi., 1897.

PLATES XVII.–XXIII.

EXPLANATION OF FIGURES.

Fig. 54.	Pig embryo,	40 days, 52 mm.	Posterior view.	× 2.
Fig. 55.	,,	40 days, 52 mm.	Left lateral view.	× 2.
Fig. 56.	,,	40 days, 52 mm.	Mesial sagittal section.	
Fig. 57.	,,	44 days, 64 mm.	Posterior view.	× 2.
Fig. 58.	,,	44 days, 64 mm.	Anterior view.	× 2.
Fig. 59.	,,	44 days, 64 mm.	Mesial sagittal section.	
Fig. 60.	,,	48 days, 80 mm.	Posterior view.	× 2.
Fig. 61.	,,	48 days, 80 mm.	Anterior view.	× 2.
Fig. 62.	,,	48 days, 80 mm.	Mesial sagittal section.	
Fig. 63.	,,	51 days, 88 mm.	Posterior view.	× 2.
Fig. 64.	,,	51 days, 88 mm.	Anterior view.	× 2.

Fig. 65. Pig embryo, 51 days, 88 mm.   Mesial sagittal section.
Fig. 66.   „   55 days, 100 mm.   Mesial sagittal section.
Fig. 67.   „   59 days, 118 mm.   Superior posterior view.
Fig. 68.   „   59 days, 118 mm.   Anterior view.   × 2.
Fig. 69.   „   59 days, 118 mm.   Mesial sagittal section.
Fig. 70.   „   65 days, 132 mm.   Posterior view.   × 2.
Fig. 71.   „   65 days, 132 mm.   Superior view.   × 2.
Fig. 72.   „   65 days, 132 mm.   Anterior view.   × 2.
Fig. 73.   „   65 days, 132 mm.   Left lateral view.   × 2.
Fig. 74.   „   65 days, 132 mm.   Mesial sagittal section.
Fig. 75.   „   70 days, 150 mm.   Superior view.   × 2.
Fig. 76.   „   165 mm.   Posterior view.   × 2.
Fig. 77.   .,   165 mm.   Superior view.   × 2.
Fig. 78.   „   165 mm.   Left lateral view.   × 2.
Fig. 79.   „   165 mm.   Anterior view.   × 2.
Fig. 80.   „   165 mm.   Mesial sagittal section.
Fig. 81. Pig, adult.   Anterior surface.   × 1.
Fig. 82.   „   „   Superior view.   × 1.
Fig. 83.   „   „   Posterior view.   × 1.
Fig. 84.   „   „   Mesial sagittal section.   × 1.
Fig. 85. Mustela furo.   Anterior surface.   × 2
Fig. 86.   „   Superior view.   × 2.
Fig. 87.   „   Posterior view.   × 2.
Fig. 88.   „   Mesial sagittal section.
Fig. 89. Meles taxus.   Anterior surface.   × 1
Fig. 90.   „   Superior view.   × 1.
Fig. 91.   „   Posterior view.   × 1.
Fig. 92.   „   Mesial sagittal section.
Fig. 93. Canis familiaris.   Anterior surface.   × 1.
Fig. 94.   „   Superior view.   × 1.
Fig. 95.   „   Inferior surface.   × 1.
Fig. 96.   „   Mesial sagittal section.
Fig. 97. Canis vulpes.   Superior view.   × 1.
Fig. 98.   „   Posterior view.   × 1.
Fig. 99.   „   Mesial sagittal section.
Fig. 100. Cat.   Superior view.   × 1.
Fig. 101.   „   Posterior view.   × 1.
Fig. 102.   „   Mesial sagittal section.   × 1.
Fig. 103. Ovis aries.   Anterior view.   × 1.
Fig. 104.   „   Posterior view.   × 1.
Fig. 105. Goat.   Mesial sagittal section.   × 1.
Fig. 106. Bos taurus.   Mesial sagittal section.   × $\frac{1}{2}$.
Fig. 107. Equus caballus.   Anterior superior view.   × $\frac{1}{2}$.
Fig. 108.   „   Posterior view.   × $\frac{1}{2}$.
Fig. 109.   „   Mesial sagittal section.   × $\frac{1}{2}$.

FIG. 47.

FIG. 48.

FIG. 49.
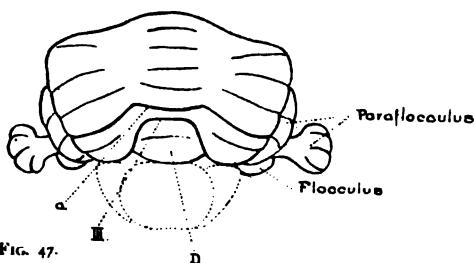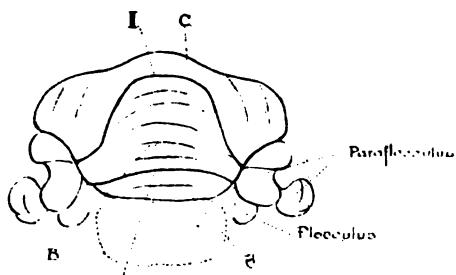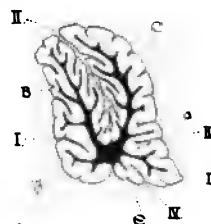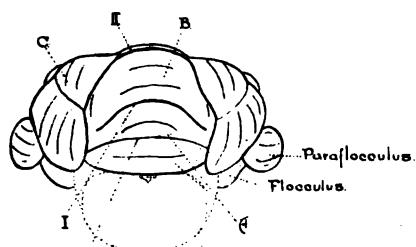
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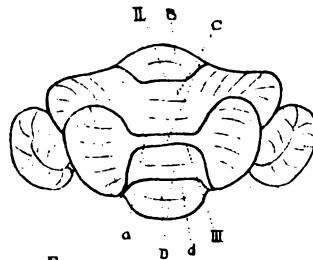
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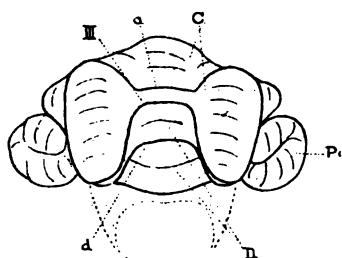
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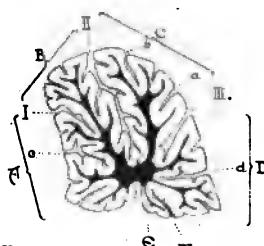
FIG. 53.

Professor O. CHARNOCK BRADLEY on the Development and
Homology of the Mammalian Cerebellar Fissures.
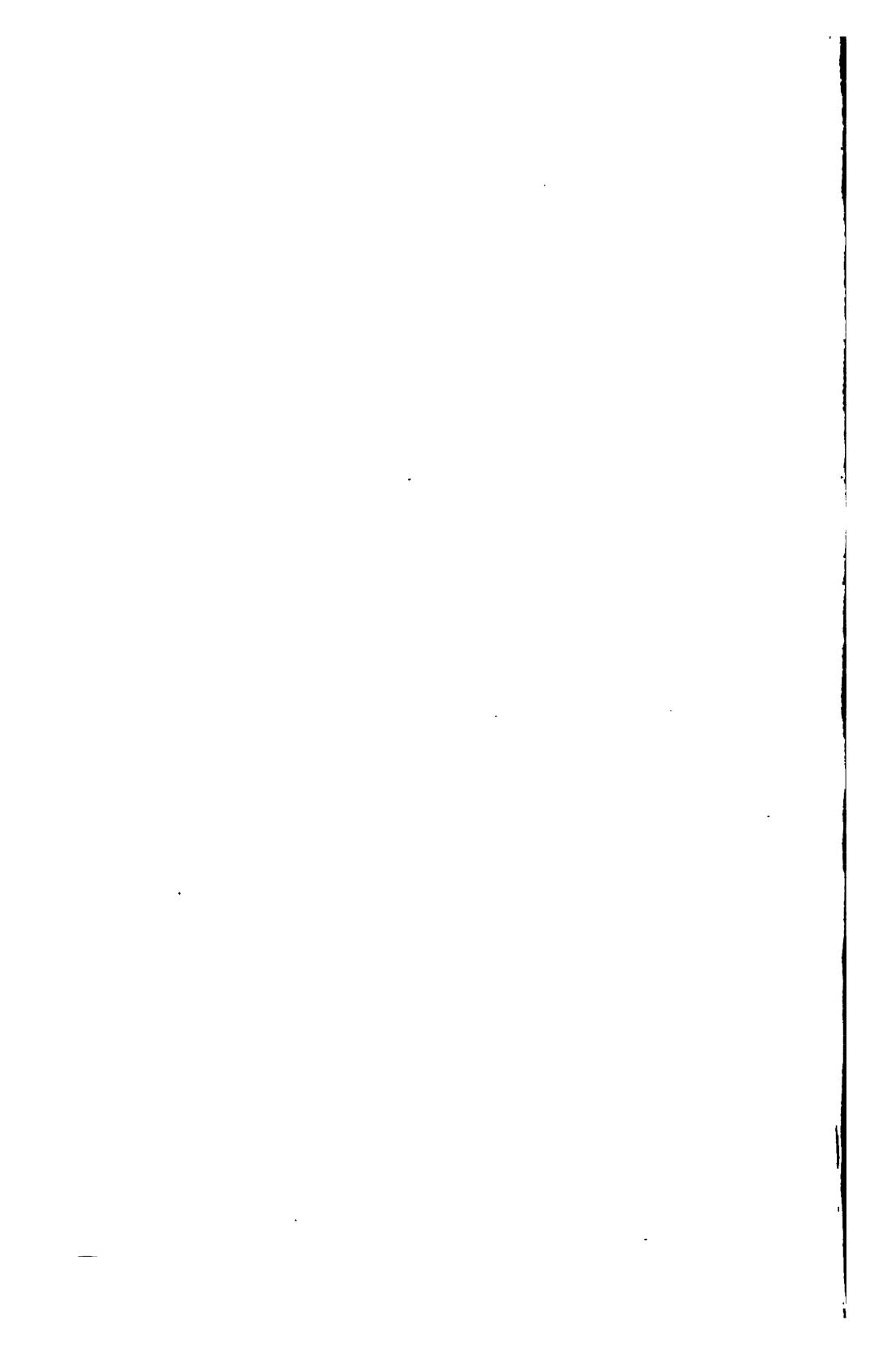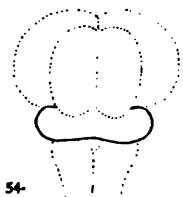
FIG. 54.

FIG. 55.
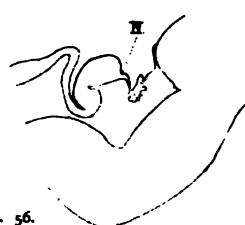
FIG. 56.

FIG. 57.
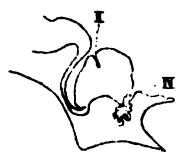
FIG. 58.

FIG. 59.
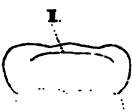
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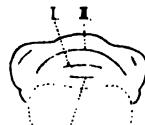
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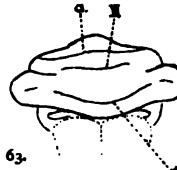
FIG. 62.

FIG. 63.
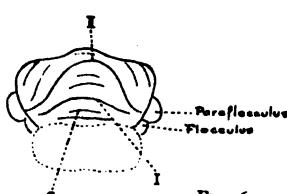
FIG. 64.

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Homology of the Mammalian Cerebellar Fissures.

[PLATE XIX.

FIG. 65.

FIG. 66.

FIG. 67.

Parafloccilus

FIG. 68.

Parafloccilus
Flocculus

FIG. 69.

FIG. 70.

FIG. 71.

Paraflocculus.
Paraflocculus.
Flocculus.

FIG. 72.

Paraflocculus.

FIG. 73.

Flocculus.

FIG. 74.

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Homology of the Mammalian Cerebellar Fissures.

[PLATE XX.

FIG. 75.   FIG. 76.   FIG. 77.

FIG. 78.   FIG. 79.

FIG. 80.   FIG. 81.

FIG. 82.   FIG. 83.
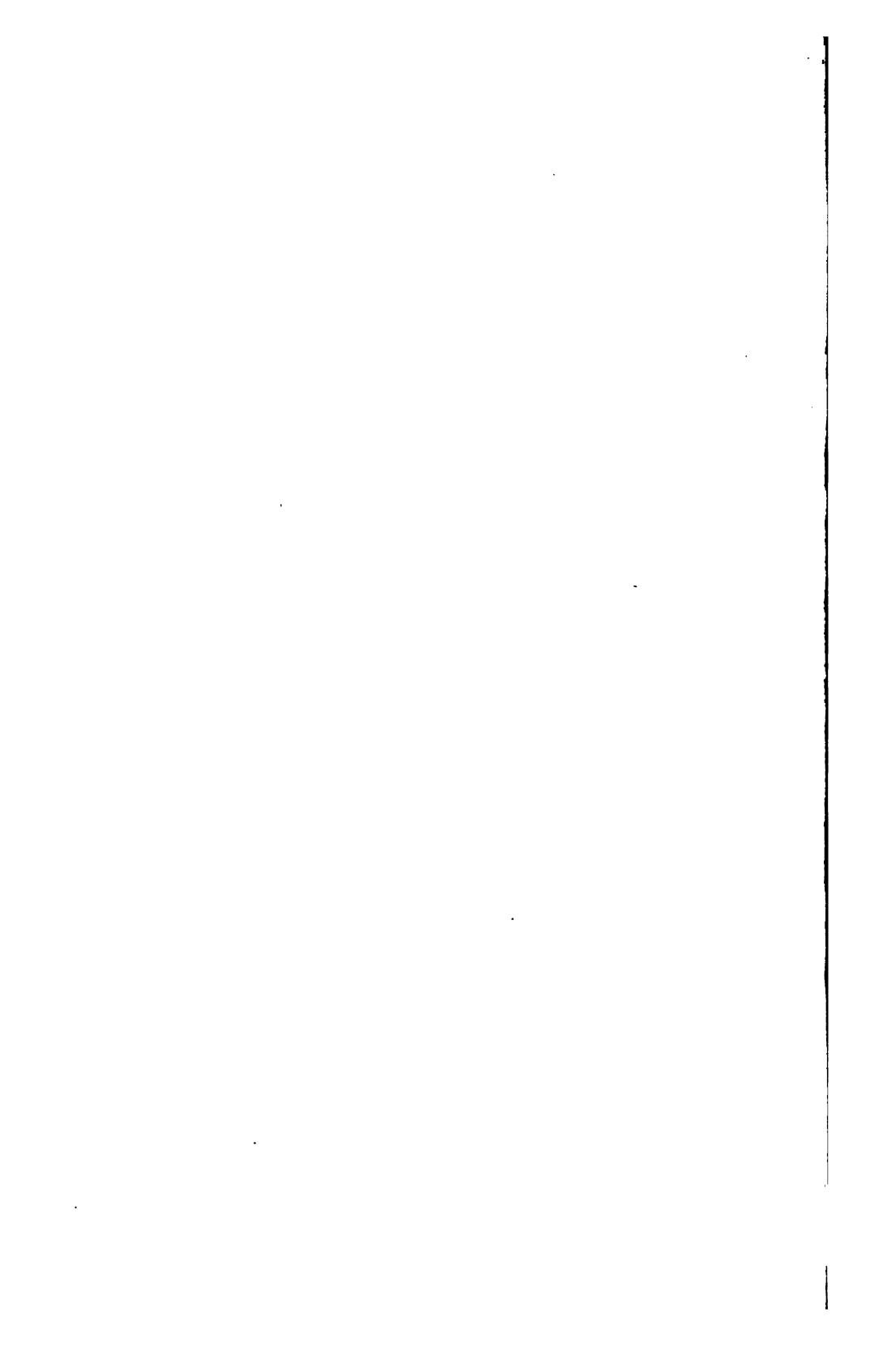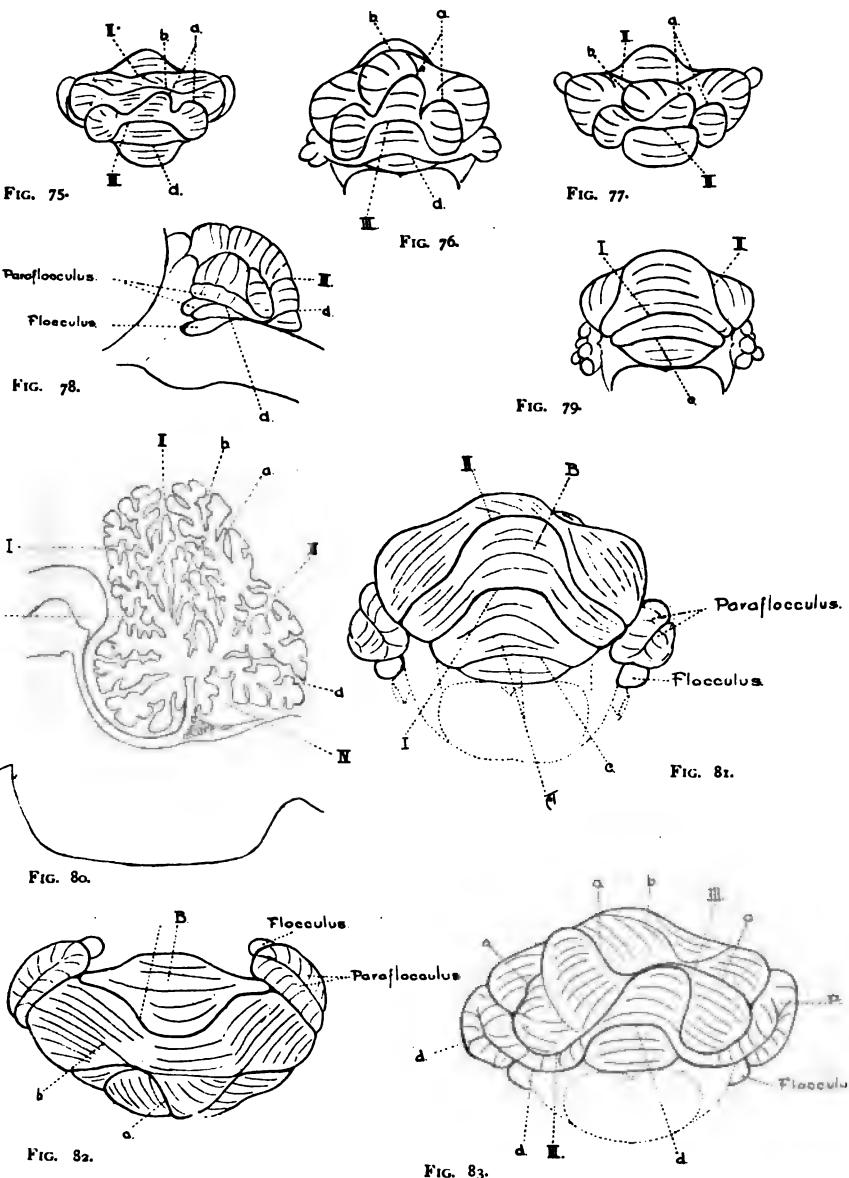
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Homology of the Mammalian Cerebellar Fissures.

FIG. 84.

FIG. 85.
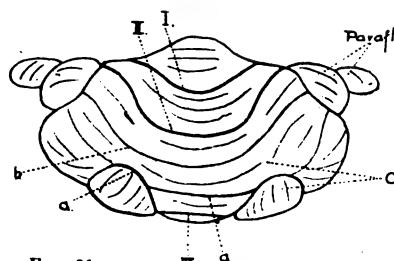
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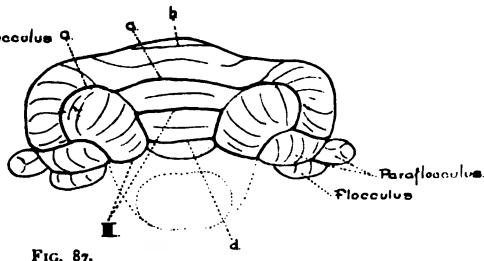
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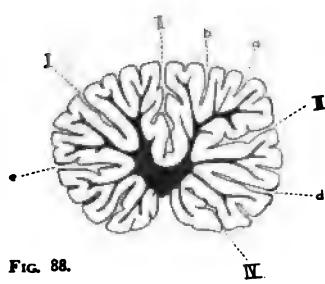
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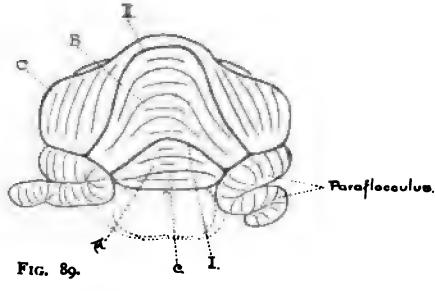
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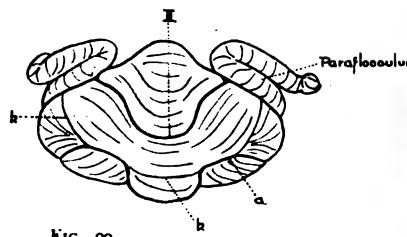
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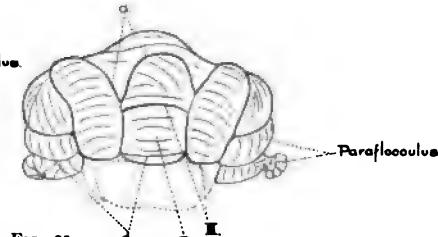
FIG. 91.

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Homology of the Mammalian Cerebellar Fissures.

[PLATE XXII.
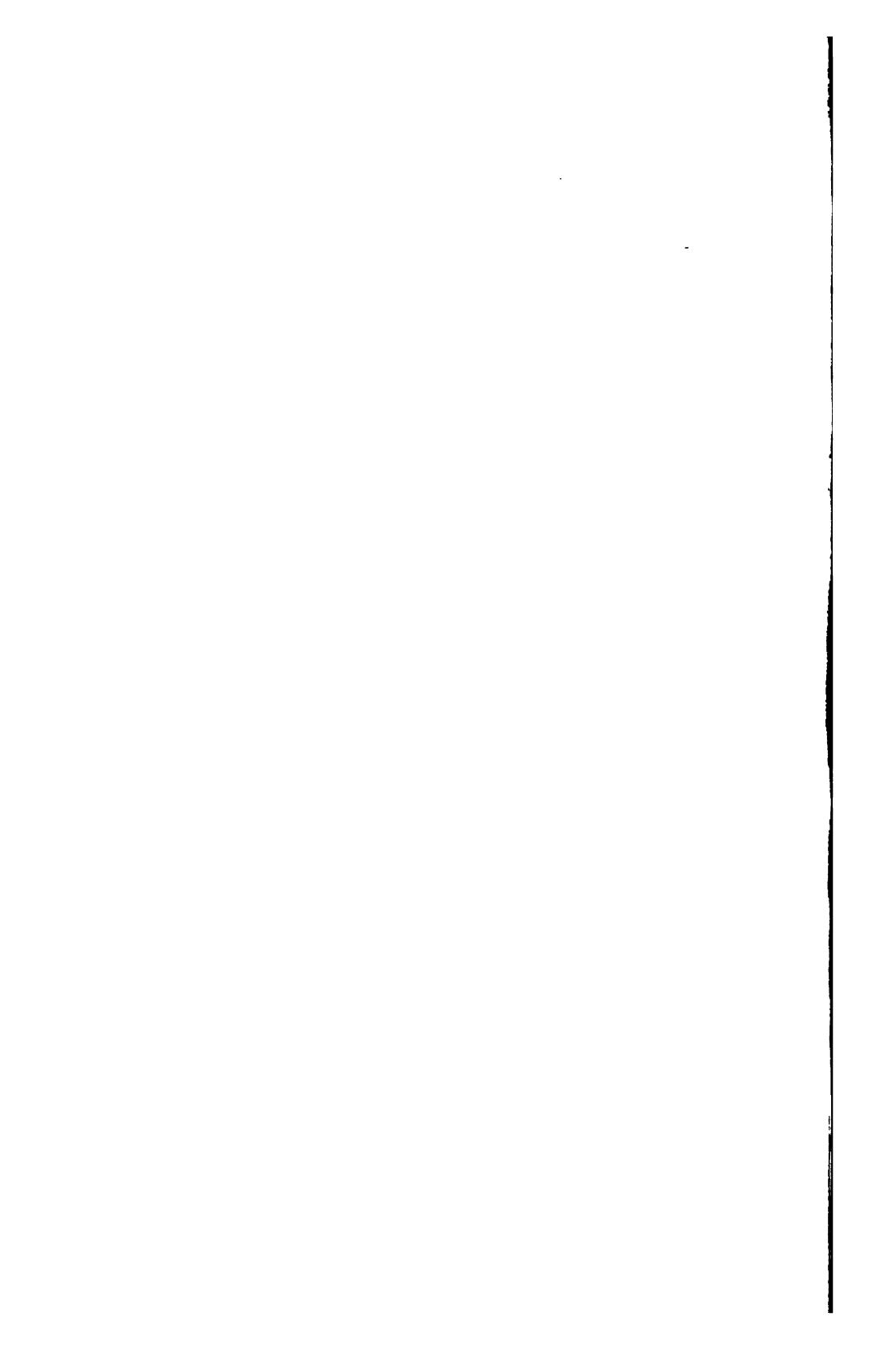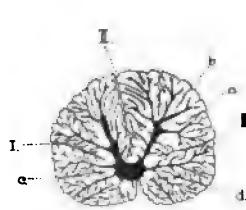
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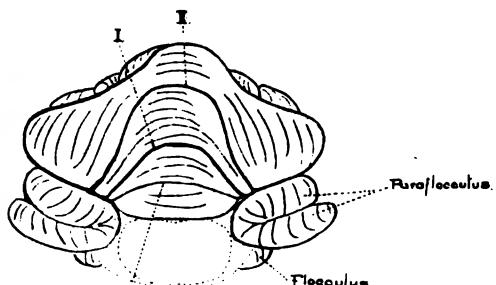
FIG. 93.
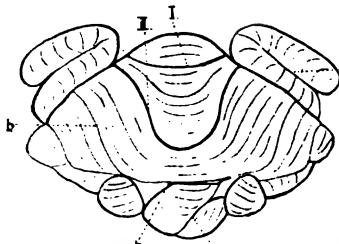
FIG. 94.
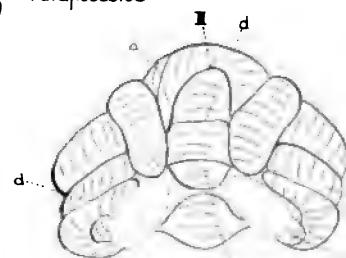
FIG. 95.

FIG. 96.

FIG. 97.

FIG. 99.
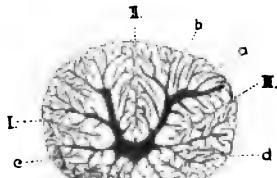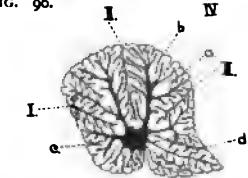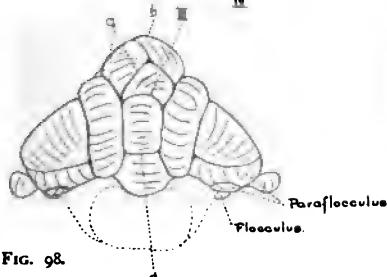
FIG. 98.
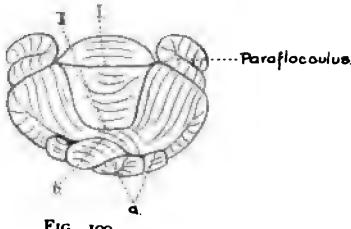
FIG. 100.

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Homology of the Mammalian Cerebellar Fissures.
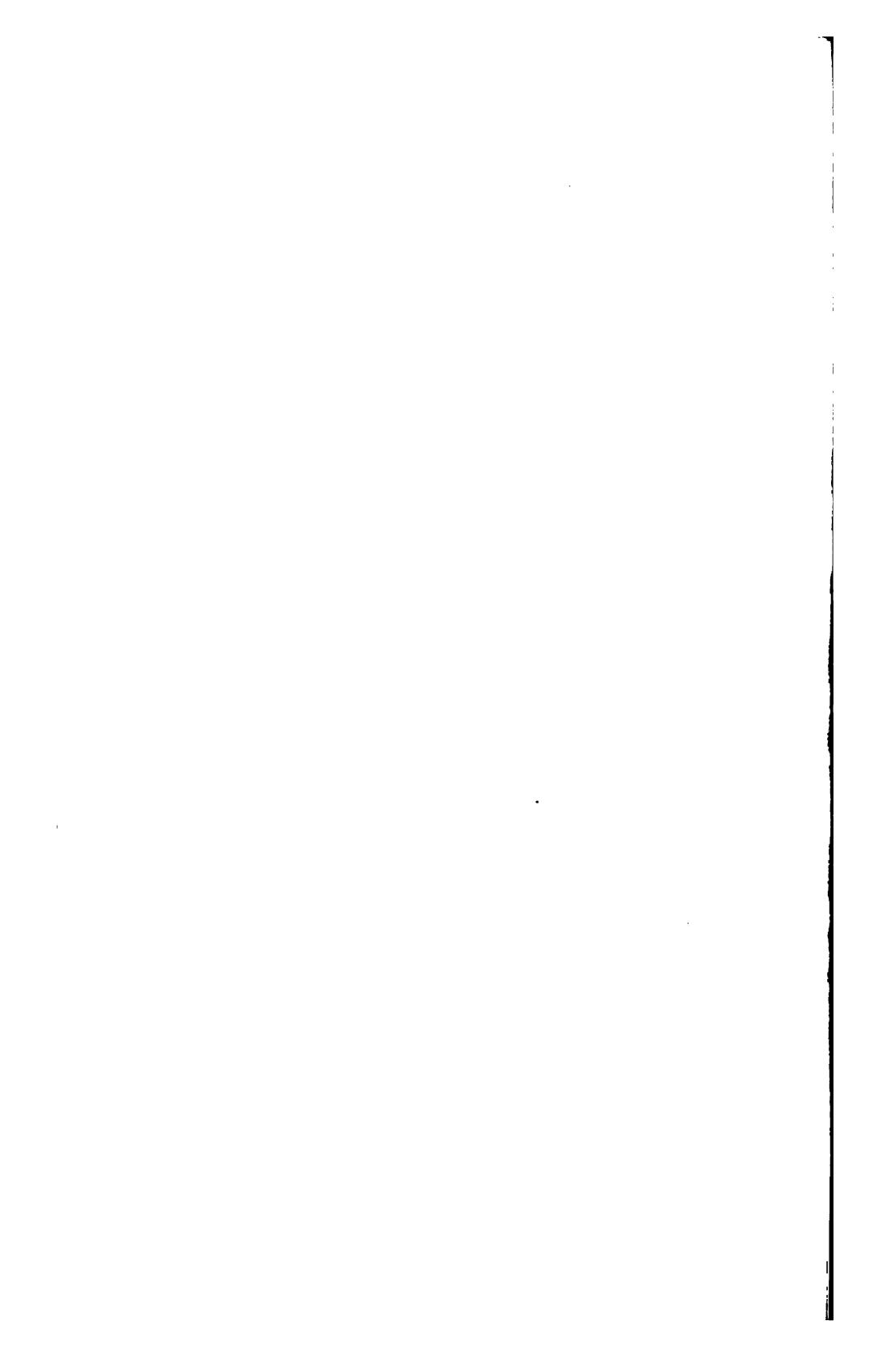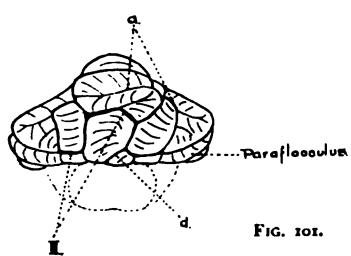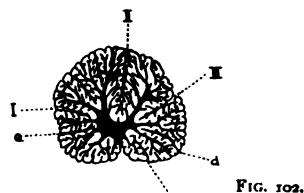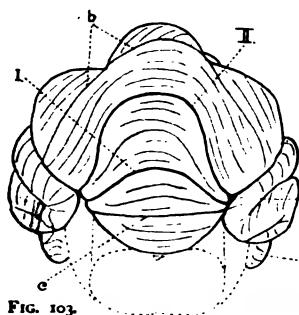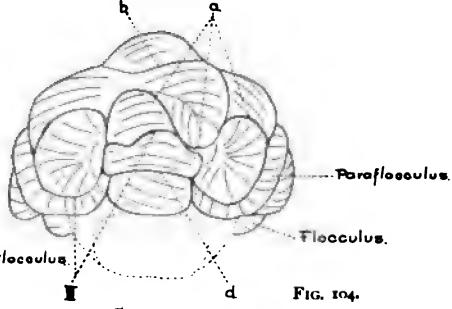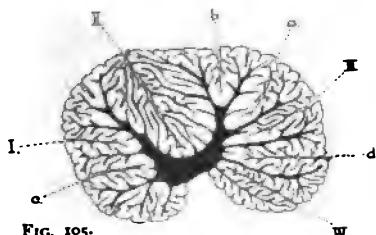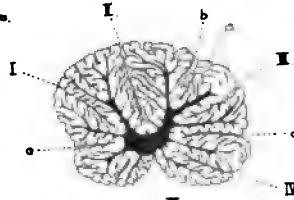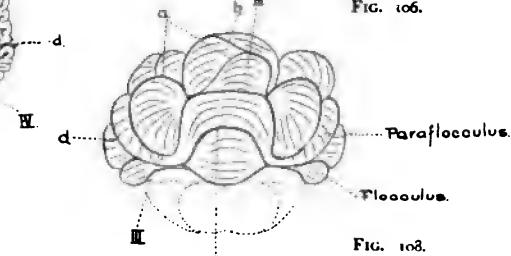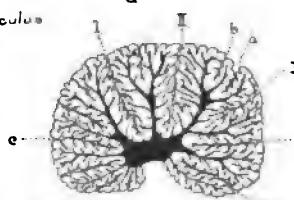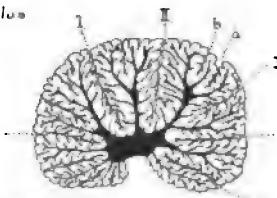
Professor O. CHARNOCK BRADLEY on the Development and
Homology of the Mammalian Cerebellar Fissures.
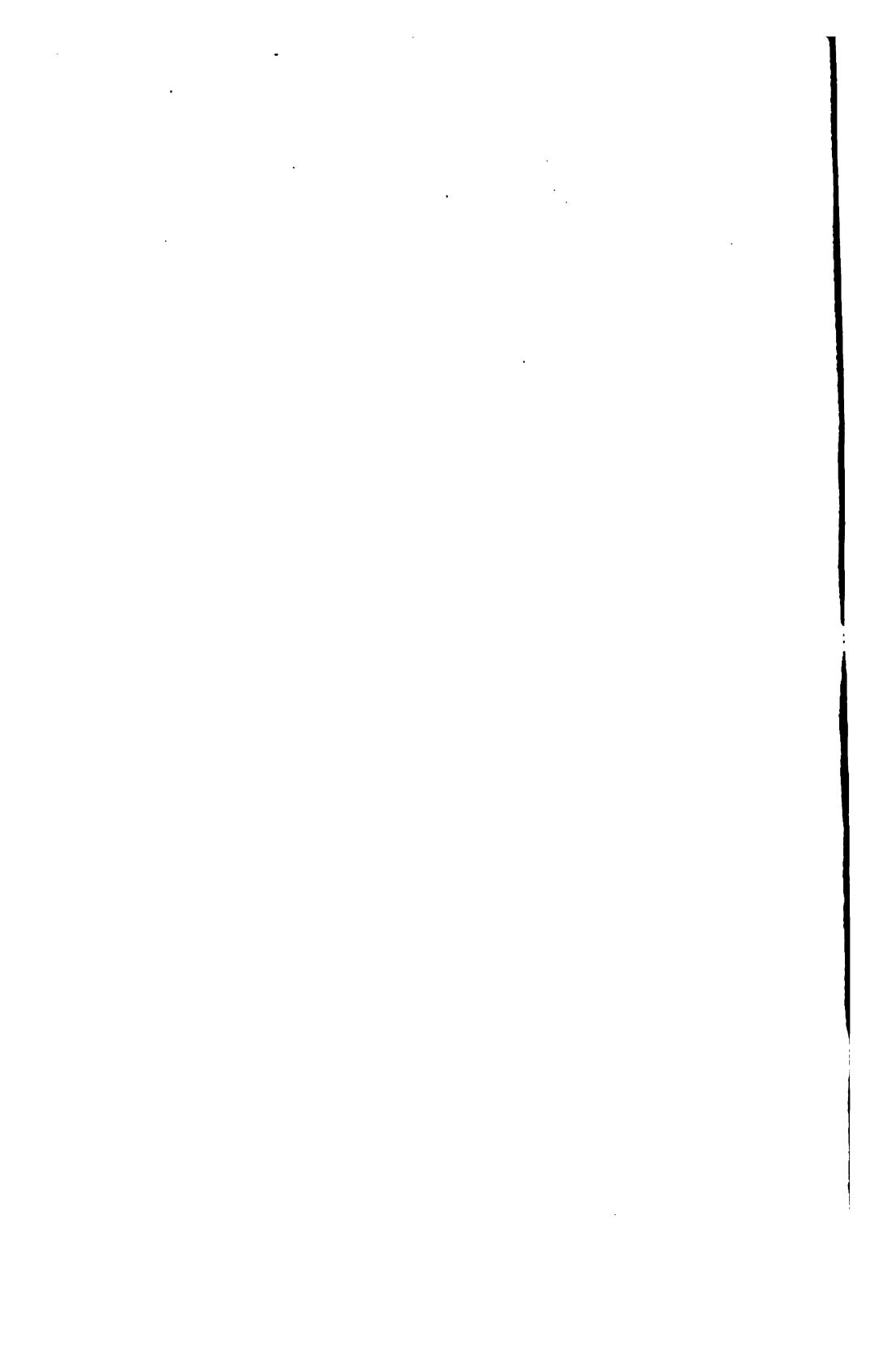
OBSERVATIONS ON THE RELATIONS OF THE DEEPER
PARTS OF THE BRAIN TO THE SURFACE. By
JOHNSON SYMINGTON, M.D., *Professor of Anatomy, Queen's
College, Belfast.* (PLATES XXIV.-XXIX.)

WHILE the literature dealing with the position of the cerebral
fissures and convolutions in relation to the external surface of
the skull and the scalp is very extensive, much less attention
has been devoted to the study of the superficial relations of the
deeper parts of the brain. This is mainly due to the fact that
the cerebral cortex is now recognised as being within the terri-
tory of ordinary surgical operative work, while the deeper parts
are in the main a hinterland still unexplored by the surgeon's
knife. A study of the surface relations of the more deeply
placed structures, however, is not only of anatomical interest,
but may prove of practical importance in determining the
structures involved in deep wounds of the brain, such as gun-
shot injuries, etc.

A considerable number of drawings have been published of
sections through the entire head, but they are usually limited
to one or two sections through the same head, and thus only
indicate the position of a limited number of the deeper structures,
and these in only a small part of their extent. The extensive
series of photographs of the brain cut *in situ* which are to be
found in Macewen's *Atlas of Head Sections* forms a striking
exception to this statement; but even in this work the absence
of figures giving surface views of the various heads examined,
marked so as to show the planes of the sections in relation to
the surface and the position of the structures between the
various sections, diminishes considerably its practical value.

The important work of Professor Alec Frazer [1] gives more
information on this subject than any other with which I
am acquainted, but a number of the deeper structures are in-
distinctly represented. Both Macewen's and Frazer's investi-

[1] *A Guide to Operations on the Brain*, London, 1890.

gations suffer from the fact that they were undertaken before the introduction of formol as a fixing and hardening agent.

In this paper I propose to give the results of a study of the relations of the brain to the skull and scalp in an adult female, by a plan I demonstrated and described some years ago.[1] It is intended to serve as an illustration of this method, as well as form a contribution to our knowledge of the surface relations of the deeper parts of the brain.

In the last number of this Journal I referred to the specimen about to be described in a paper entitled " Are the cranial contents displaced and the brain damaged by freezing the entire head ? " and I gave a photograph (see pl. xi.) of a median section of part of the brain. I trust that the present communication will contain additional proof in support of my contention that the freezing process does not necessarily distort or displace the brain in the cranial cavity.

The results obtained from the study of this head are given in the illustrations accompanying this paper, and in the following description of each plate.

PLATE XXIV.

This is from a photograph of the right side of the head of a female 54 years old. The circumference of the cranium, measured at the level of the glabella and the occipital point, was 20 inches. Its length from nasion to occipital point was $7\frac{1}{4}$ inches, and the biparietal diameter was $5\frac{5}{8}$ inches, giving a breadth index of 79, so that it comes very nearly within the brachycephalic group. The height, from basion to bregma, was $5\frac{1}{8}$ inches, giving a height index of 72.

The photograph was taken after the head had been frozen and cut into six slabs. These were replaced in their proper order, with sheets of cardboard between them to represent the thickness of the tissue removed by the saw. Care was taken to obtain a correct profile view; and to secure an orthogonal projection of the peripheral parts, the head was placed between 5 and 6 feet from the lens. The photograph obtained was enlarged to life size.

THE SKULL.—The soft parts were cut in the median plane down to the bone, and removed on the right side from the five upper slabs so as to expose the surface of the skull. Another photograph was then taken in the same position as the skin view, and from a full-size enlargement of this a tracing was taken, so that the position of the cranial sutures could be outlined upon the first photograph. In.

[1] *Proceedings of the Royal Academy of Medicine in Ireland*, vol. xvi. p. 407.

this plate the articulations of the parietal bone in front, behind, and below are shown. Behind the upper extremity of the great wing of the sphenoid (G.W.S.) there is an epipteric bone. The median cut surfaces of the vaulted part of the skull from the glabella to the posterior margin of the foramen magnum, of the basi-occipital and basi-sphenoid, and of the atlas and axis, have been projected on to the side of the head. The external occipital protuberance is indistinctly marked, but from the muscular attachments its position is indicated by a × on the lower part of slab 4. The position of the median boundaries of the nasal part of the pharynx and the soft palate, as well as the pharyngeal orifice of the left Eustachian tube, are outlined on the side of the face.

THE BRAIN.—In this plate an outline is given of the structures visible on the left half of the median section of the brain. It was constructed as follows :—Upon the upper surfaces of each slab, from the second downwards, lines were drawn outwards at right angles to the median plane on to the surface, so as to mark the position on the lateral aspect of the head of the median portions of the brain. Each slab was afterwards divided into right and left halves, and a tracing of the structures exposed in the left half of each slab was transferred to the corresponding slab in the right profile photograph.

The antero-posterior arch of the corpus callosum is very well marked, and also the vertical descent of its splenial end. A horizontal line uniting points opposite the anterior and posterior extremities of the corpus callosum is barely 2½ inches in length, and the highest part of the corpus callosum is 1 inch above a line uniting the lower ends of the genu and the splenium. The whole of the median portion of the corpus callosum is covered by that portion of the parietal bone which assists in the formation of the floor of the temporal fossa, and its highest portion is about half an inch below the top of the temporal ridge. The genu does not reach quite as far as the coronal suture, and the splenium is about opposite a vertical line prolonged upwards from the posterior border of the mastoid process. The antero-posterior extent of the corpus callosum in this specimen is rather less than the average for an adult brain hardened *in situ*, where it is generally 3 inches. In an adult male I found the genu of the corpus callosum to reach nearly a quarter of an inch in front of the coronal suture, and also to be a little lower than in this specimen. On an average, we may consider that the genu of the corpus callosum extends to the level of the lower part of the coronal suture. Frazer, in his *Guide to Operations on the Head*, has two plates, viz., xi. and xxiv., with composite photographs of the head of a female 38 years old, from which it would appear that the genu not only reached in front of the coronal suture, but also downwards so as to be overlapped by the upper extremity of the great wing of the sphenoid. In this case, however, the sutures in the region of the pterion are indistinctly marked, and the great wing appears to be prolonged upwards and backwards farther than usual.

The portion of the 3rd ventricle above the sulcus of Monro lies above a line uniting the apex of the rostrum and the extremity of the

splenium of the corpus callosum, and is covered by the parietal bone. The lower or infundibular portion of this ventricle (3'), on the other hand, is under the squamous portion of the temporal bone. Its long axis is directed downwards and forwards, and is fully an inch in length.

The long axis of the medulla and pons is practically vertical. The junction of these two parts of the brain is opposite the roof of the external auditory meatus, and about the same level as the vault of the nasal part of the pharynx. A horizontal line 1 inch above the top of the external auditory meatus will mark the level of the upper limit of the pons Varolii, and another half inch higher the top of the pons Tarini uniting the two crura cerebri.

The median lobe of the cerebellum is covered by the parietal, temporal and occipital bones. Its upper extremity, which is a little behind and at the level of the lowest part of the splenium of the corpus callosum, represents the highest part of the whole cerebellum. Its lower end, however, does not reach so low as the lateral lobe (L.L.), for the inner surface of the amygdalus extends into the foramen magnum as far down as a line uniting the lowest parts of the anterior and posterior boundaries of this aperture. The height of the median lobe of the cerebellum is 2 inches, and a line directed downwards and forwards from the top of the superior vermis to the lower end of the amygdalus measures $2\frac{3}{4}$ inches.

The principal fissures on the mesial aspect of the left cerebral hemisphere are indicated by dotted lines. The fissure of Rolando (F.R.) turns round the superior mesial border $1\frac{3}{4}$ inches behind the bregma, and is prolonged downwards and backwards for a distance of little more than half an inch. The parieto-occipital fissure (P.O.F.) cuts the mesial border at the same horizontal level as the apex of the lambdoidal suture. The part of the calcarine fissure (C.F.) behind the union of this fissure with the parieto-occipital is just above the border separating the mesial from the tentorial surface of the occipital lobe. It will be seen that, viewed from the lateral aspect, nearly the whole of the cuneate lobule is covered by the parietal bone.

<div align="center">PLATE XXV.</div>

This plate shows the position of the fissures and convolutions on the lateral aspect of the right cerebral hemisphere to the cranial bones and sutures, and also that of the right lateral, the third and the fourth ventricles in relation to both the cranium and the convolutions.

It will be seen from the view of the skull that the sections of this head were not made quite parallel to the ear-orbital line, i.e. a line uniting the highest part of the external auditory meatus with the lowest part of the margin of the orbit. A skull so placed as to have this line horizontal is generally regarded as being in a horizontal position, and consequently the plane of the sections through this head are directed from the front backwards and a little downwards, so as to make an angle open to the front of about 10 degrees with the

horizontal plane. This does not, of course, affect the accuracy of the orthogonal projections of the deeper structures on to the side of the head.

Professor A. Froriep[1] has divided the variations in the position of the cerebral hemispheres in relation to the skull into two main groups, which he names frontopetal and occipitopetal. In the former, the brain lies farther forwards; in the latter, it may be supposed to have been pressed backwards, and the occipital pole depressed. In order to illustrate the differences between these two groups, a line is drawn from the lowest part of the margin of the orbit backwards through the highest part of the external auditory meatus. From this horizontal base line another is drawn vertically upwards from the centre of the external auditory meatus. In the frontopetal type the vertical line crosses the fissure of Rolando further forwards, and the occipital lobe is higher in relation to the horizontal line than in the occipitopetal type. This brain belongs to the frontopetal type. Thus the general direction of the lower border of the temporo-occipital part of the hemisphere is backwards and upwards when compared with the ear-orbital line, so that the lowest part of the occipital lobe is nearly 2 cm. above this line.

The Sylvian point, the spot where the Sylvian fissure is seen on the lateral aspect of the brain dividing into its anterior and posterior branches, is a trifle higher up and farther back in relation to the pterion than usual; still the position of the Sylvian fissure may be regarded as well within the range of normal variations.

The fissure of Rolando measured in a straight line on the surface of the brain from the superior mesial border of the hemisphere to its termination above the Sylvian fissure is $3\frac{1}{2}$ inches long. In a profile view it is $2\frac{1}{4}$ inches. This difference is, of course, due to its passing outwards as well as forwards and downwards; thus, at the upper surface of slab 2, the fissure is 2 inches from the median plane.

The literature dealing with the relations of the lateral ventricles to the surface of the brain and skull is scanty, and refers chiefly to the question of the best surgical route to its cavity.

In plate xxi. Frazer[2] has an excellent view of the lateral ventricles exposed from the right side, with the central lobe and the caudate nucleus still *in situ*. In consequence of these structures not having been removed, only the outer border of the body of the lateral ventricle is visible, but the three horns are distinctly seen, all of them being well developed, more especially the posterior one. Professor Thane[3] has a diagram of an outline of the cavity in relation to the side view of the skull and of the Rolandic and Sylvian fissures, but otherwise our anatomical text-books do not attempt to indicate its position with reference to the surface. Mr E. A. Spitzka[4] recently

[1] *Die Lagebeziehungen zwischen Grosshirn und Schädeldach*, Leipzig, 1897.
[2] *Op. cit.*, p. 241.
[3] *Quain's Anatomy*, Appendix, 10th edition, 1896, fig. 5.
[4] A preliminary communication, with projection drawings illustrating the topography of the paracœles (lateral ventricles) in their relation to the surface of the cerebrum and the cranium, *New York Med. Journ.*, 2nd Feb. 1901.

published a short paper giving the results of his examination of two adult heads. He gives a full-size outline (fig. 1) of a side view of the skull of one of these heads, with the convolutions and lateral ventricle, and similar outlines (figs. 4 and 5) of both sides of the other head he investigated. The brains were hardened *in situ*, removed from the cranial cavity and divided in a coronal direction into sections a quarter of an inch thick. No explanation is given as to how the relations between the skull and the brain were determined, and from an examination of Spitzka's drawings I must confess that their accuracy in this respect is very doubtful. Thus, in fig. 1, a base line is drawn from the external angular process of the frontal straight to the inion. This line is figured as passing just below the external auditory meatus, whereas, in a normal skull, it would go above the auditory meatus, as it does when marked upon his figs. 4 and 5. Again, in fig. 1, the lower limit of the temporal lobe of the brain crosses the external auditory meatus just below its upper border, and the descending horn is depicted as only a quarter of an inch above the level of the upper border of the meatus. His drawing thus ignores the existence of a thick bony roof to the meatus, or an attic to the tympanic cavity.

In *this Journal* Dr J. O. Wakelin Barratt[1] gives a drawing (fig. 2) of a profile view of the left side of the brain, with the relations of the lateral and third ventricles to the convolutions. Barratt's figure may be compared with that of this plate, but it must be noticed that the 'horizontal' line he marks on the brain would be by no means parallel with the ear-orbital line of the skull. The frontal end of the brain is tilted downwards so that it reaches fully as low as the occipital lobe, and the posterior horn of the lateral ventricle is about as high as the body of the lateral ventricle.

In my specimen the cavities of both lateral ventricles are rather small, especially in their cornual portions. On the right side the highest part of the body of the ventricle, which is formed by its outer border, is 3 inches above the roof of the external auditory meatus, half an inch below the highest part of the temporal ridge, and 2 inches from the top of the head. The anterior cornu formed a mere slit in front of the head of the caudate nucleus; but had it been dilated to a degree frequently met with in normal brains, it would have reached as far forwards as the coronal suture.

If pl. xxi. of Frazer's work,[2] showing a profile view of the left lateral ventricle, be compared with his pl. ii. containing a view from the same aspect of the surface of the skull, the anterior horn will be found to reach as far as this suture. Thane[3] figures this horn as projecting fully half an inch in front of this suture, but a position so far forwards is probably unusual, unless it be abnormally distended. The posterior horn is so variable in its development that it is difficult to strike an average. In my specimen it is certainly narrower and

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[1] "The form and form-relations of the human cerebral ventricular cavity," *Jour. Anat. and Phys.*, vol. xxxvi., Jan. 1902.

[2] *Op. cit.*, p. 241.   [3] *Op. cit.*, p. 245.

shorter than usual.   The cavity of the descending horn was little more than a slit, and in a diagram indicating its average size my outline would require to be slightly thickened and lengthened.   The most important part of the ventricle from a surgical point of view is where the body turns downwards and outwards, to end in the descending and posterior horns.   Its cavity is not liable to be reduced to a mere slit, as is the case with nearly all the other parts of the lateral ventricle, and, with the exception of the upper part of the descending horn, it is nearer the lateral surface of the brain than any other part of the ventricle; hence it is the portion selected for tapping or injecting the ventricle.   This region is marked in this plate by a circular spot, and it is shown in section in Pls. XXVI. and XXVII. In my specimen it is opposite the posterior part of the superior temporal convolution, about an inch behind and 2 inches above the external auditory meatus.   Dr Keen's[1] point for reaching the ventricle is 1¼ inches above and behind the external auditory meatus.

The surface relations of the 3rd and 4th ventricles are represented in Pl. XXIV. as well as in this plate.   No attempt has been made to give the position of the lateral extension of the 4th ventricle.

Professor Gustaf Retzius,[2] in his beautiful illustrations of casts of the ventricles, gives a side view (fig. 1) of the lateral ventricle, with the depression for the caudate nucleus shaded.   The head of this nucleus lies external to the anterior horn and to the anterior part of the body of the lateral ventricle, and its tail follows the curve of the upper border of the descending horn.   From this plate, therefore, the position of the caudate nucleus can be determined.   It will be noticed that the outline of the anterior horn of the lateral ventricle shows in the lower part of its anterior border a concavity directed forwards.   Instead of this concavity the head of the caudate nucleus would show a convexity.

PLATE XXVI.

This is from a tracing of the upper surface of slab 3.   The plane of this section is seen in profile in Pls. XXIV., XXV. and XXIX., and, as already explained, it is not quite horizontal, being a little higher behind than in front.   The section is so typical of one commonly used to illustrate the form and relations of the nucleus caudatus (N.C.), optic thalamus (O.T.), internal capsule (Int. Cap.), nucleus lenticularis (N.L.), external capsule, claustrum, and island of Reil, as to render any detailed description unnecessary.   The island of Reil is cut a little below its superior limiting sulcus, and opposite its greatest antero-posterior extent.   On the right side the convolutions of the fronto-parietal operculum lying above the island of Reil (I. of R.) and the superior temporal convolutions (S.T., S.T.), which were

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[1] Buck's *Reference Handbook of the Medical Sciences*, vol. viii., 1889.
[2] "Die Gestalt der Hirnventrical des Menschen, nach Metallausgüssen dargestellt," *Biologische Untersuchungen*, Bd. ix., 1900.

separated from the rest of the brain in making this section, have been removed to show the latter structures. On the left side the opercula of the island of Reil were cut a little lower, and only two pieces of the fronto-parietal operculum (F.P.O.) projected below the plane of this section. The dotted lines starting from the posterior part of the body of the lateral ventricle indicate the course of the posterior and descending horns in a view from above. The descending horn usually turns more inwards at its lower and anterior extremity, but the cavity which passes towards the median plane is only a narrow cleft.

PLATE XXVII.

We have here a photograph of two sections of the brain. The one on the left side is the same as that shown on the left half of the section in Pl. XXVI., but on the right half the following dissection of slab 3 was made before the photograph was taken. The brain was divided vertically just to the right of the median plane, and the right half removed and cut horizontally 10 mm. below its upper surface. On this side also the lateral wall of the skull was removed from opposite the posterior part of the roof of the orbit backwards to the median plane. The lower part of the brain belonging to the right side was then replaced in position, and the two sections photographed together. This dissection was made more than a year after the head had been frozen and divided with a saw. It will be noticed that the surface is smoother, and the differentiation of the white and grey matter is better marked on the right side. These differences are due to the fact that the cut surface on the right side had not been subjected to much handling or exposure to the light, and also to its having been cut with a knife instead of a saw. The slight retraction of the anterior part of the left cerebrum from the skull is due to the frequent manipulation of the brain in removing and replacing it, and is not shown in the photographs taken before the brain was disturbed.

On the right section of the brain the anterior limb of the internal capsule is represented by a thin layer of fibres, so that the nucleus caudatus and the nucleus lenticularis nearly meet. Two segments of the globus pallidus (G.P.) are exposed internal to the putamen, while at the level of the left section only a small piece of one of these bodies is visible. The posterior limb of the internal capsule is still well marked. Its retro-lenticular portion (R.L.) is said to contain auditory fibres going to the superior temporal convolution (S.T.), and behind these visual fibres (O.R.), passing backwards to the occipital lobe. The splenium of the corpus callosum (C.) is divided close to its extremity, so that the fibres of the forceps major (F.M.) which come from the splenium must have curved downwards as well as backwards. The letters P.O.F. are placed behind the parieto-occipital fissure, which is exposed close to its union with the calcarine fissure.

PLATE XXVIII.

The upper surface of slab 4 is shown here. The cut separating this from slab 3 traversed the upper part of the nasal cavities and the ethmoidal air-cells (E.C.), and in the orbits exposed the optic nerves from the eyeball backwards and inwards to the optic foramina. The parts of the brain divided were the upper end of the pons Varolii, valve of Vieussens, and 4th ventricle, the cerebellum, and the temporal and occipital lobes of the brain. The upper edge of the dorsum sellæ was removed by the saw, and the 3rd nerves cut behind it, and the internal carotid arteries opened in front and to its outer side.

In the temporal lobes are seen the cavities of the descending horns (D.H.) of the lateral ventricles. They reach about as far forwards as the front of the pons, but are 1¼ inches behind the anterior extremities of the temporal lobes.

PLATE XXIX.

In this plate we have made an attempt to represent the position in relation to the side of the head of the pyramidal motor fibres from the Rolandic area, and also that of the visual tracts, together with certain parts of the brain related to these fibres. This diagram has been constructed by similar methods to those of Pls. XXIV. and XXV. already described. The outline of the skin (1) and the skull (2) are indicated by black lines, while the periphery of the cerebral hemispheres (3) and the Sylvian and Rolandic fissures are represented by interrupted lines. The outline of the cuneate lobe is taken from the left hemisphere of the brain.

Above the pons Varolii (Po.) and the superior cerebellar peduncles (S.P.) is seen the external aspect of the mid-brain, with its crus cerebri in front and the corpora quadrigemina behind. Above this is a dotted area for the optic thalamus, while the letters A and P are placed near the front and back of the internal capsule. The antero-posterior extent of the posterior limb of this capsule will, of course, correspond with the optic thalamus, external to which it lies. The mid-brain is in the lower half of slab 3, under cover of the upper part of the squamous portion of the temporal.

PYRAMIDAL FIBRES.—The letters L, A, T placed in front of the fissure of Rolando indicate generally the position of the motor centres for the leg, arm, tongue and face. E, put farther forwards, is the centre for the movements of the eye and the head. The axis-cylinder processes from the motor cells in these regions will descend in the corona radiata and then enter the internal capsule. This capsule is shown in section in Pls. XXVI. and XXVII. The pyramidal fibres are represented as traversing the knee and the anterior part of the posterior limb of the capsule. In consequence of the oblique direction of the fissure of Rolando, the leg cortical area is in a plane posterior to that

for the arm, and this again is behind the face and tongue centres. The pyramidal fibres are believed to occupy the same relative position in the internal capsule. Some of the pyramidal fibres from E may end in the mid-brain in relation to the origin of the 3rd nerve, those from T in the medulla and pons, while of course the arm and leg fibres go into the spinal cord.

When this tract is projected on to the side of the head it will be noticed that the course of its fibres is nearly vertical, although they necessarily converge as they descend. A line from the external auditory meatus to the bregma and another from the same point to the vertex about 2 inches behind the bregma would include the area occupied by these pyramidal fibres.

VISUAL FIBRES.—It was shown in Pl. XXVI. that the cut which separated the third and fourth slabs divided the eyeball and exposed the right optic nerve as far back as the optic foramen. From this opening the optic nerve passes upwards and backwards to the optic commissure, and the optic tract goes in the same direction, except that it inclines also outwards external to the interpeduncular space and the crus cerebri, to end in the lower visual centres, viz., the superior quadrigeminal bodies, the lower and posterior part of the optic thalamus and the corpora geniculata. From these lower centres fibres are represented passing backwards as the optic radiation to the cuneate lobule and the gyrus lingualis. The upper and lower limits of this optic radiation have not been precisely defined, but this tract is very distinctly seen in the section of the right side of the brain in Pl. XXVII. If other fibres pass from these parts of the cortex to an association centre in or near the angular gyrus, they must go outwards and upwards.

[Plate XXIV.

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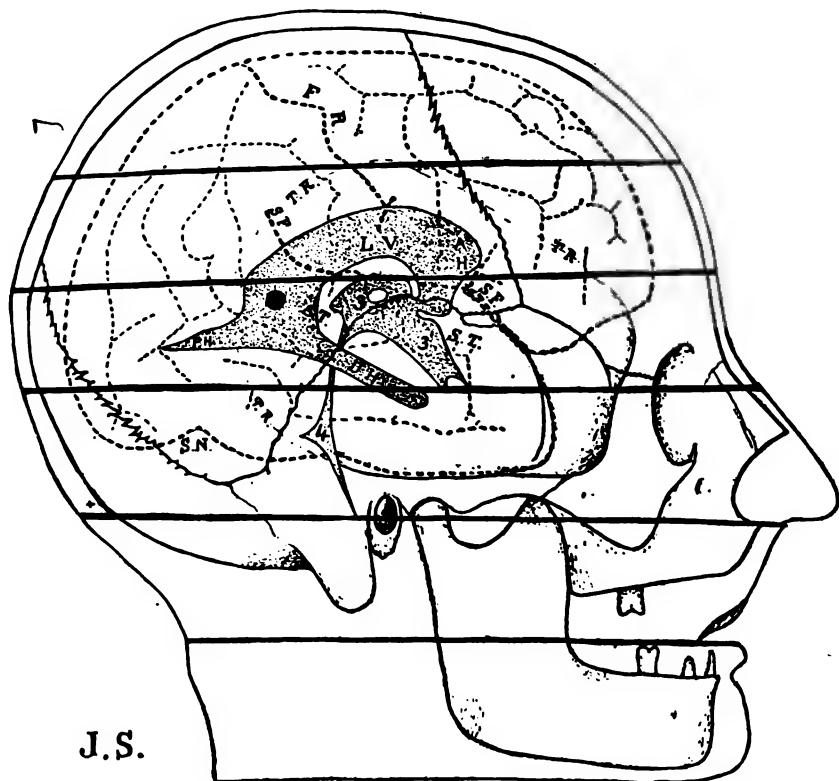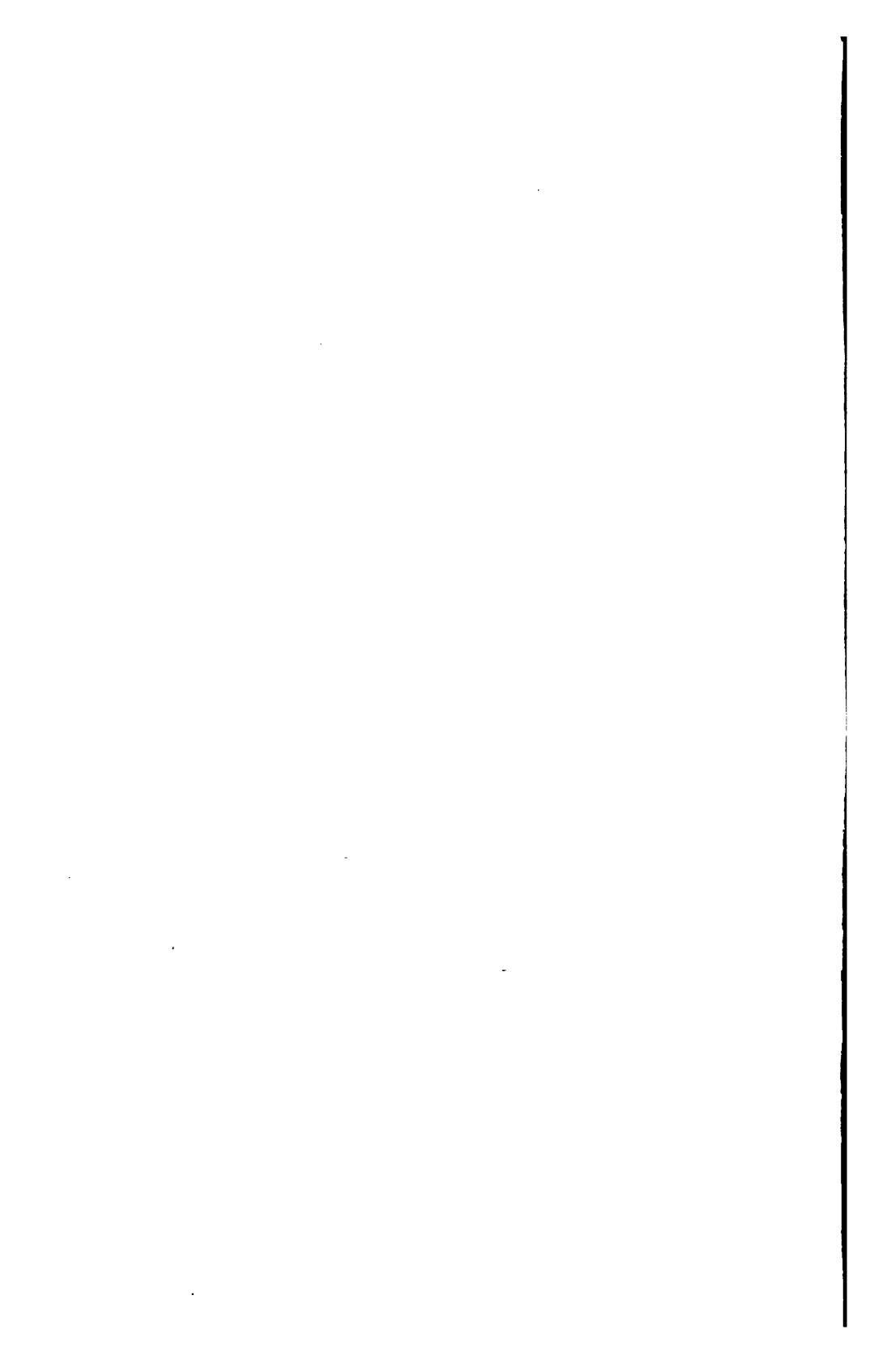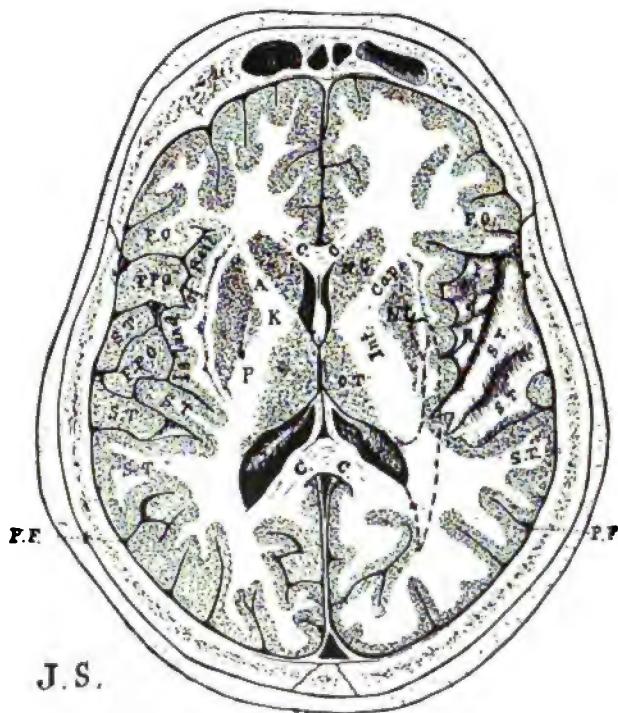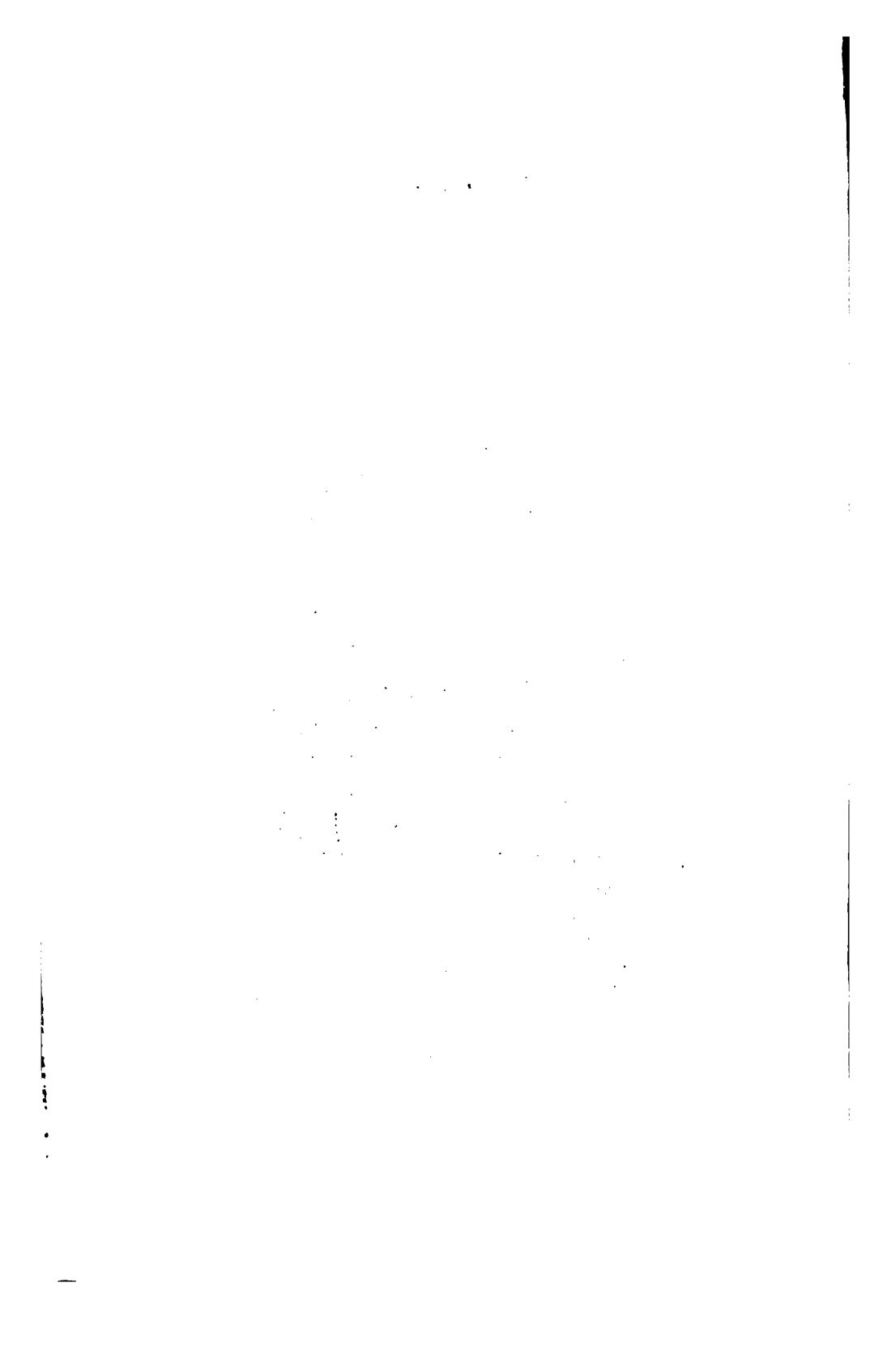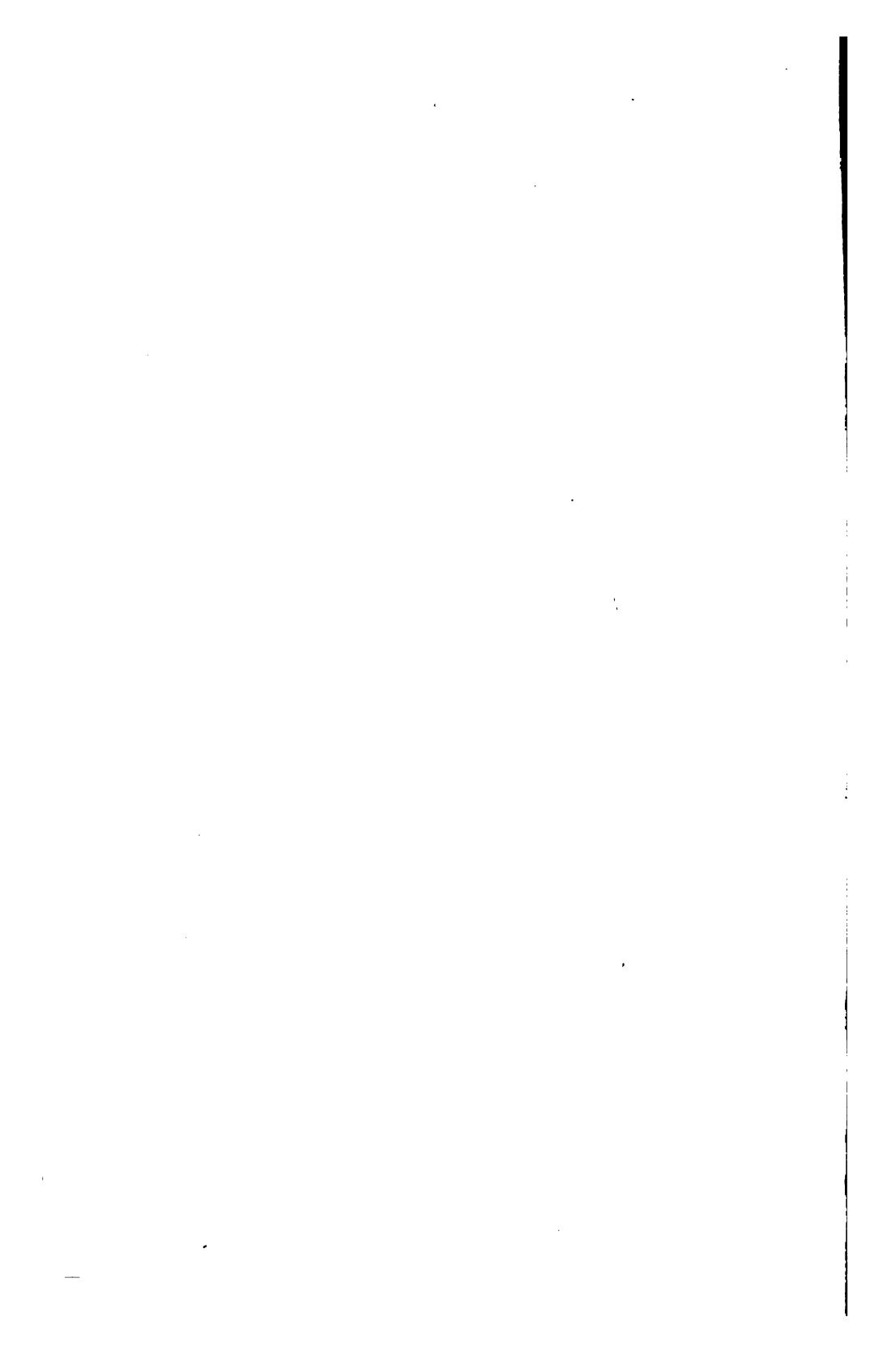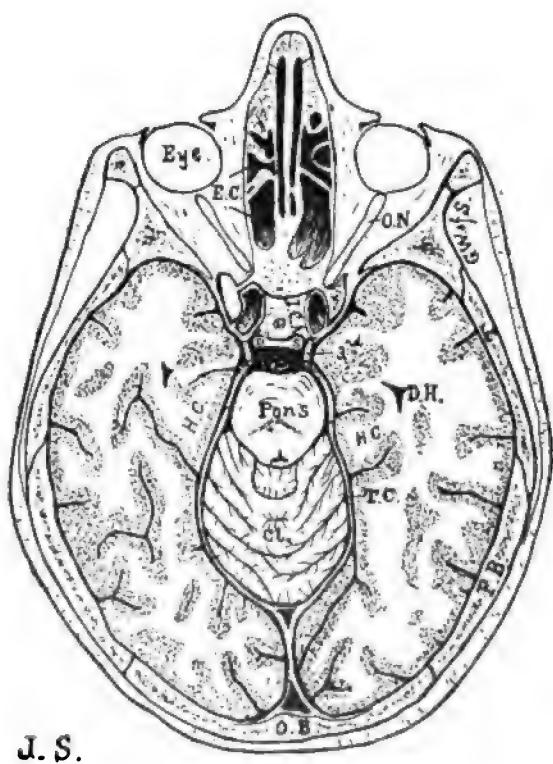
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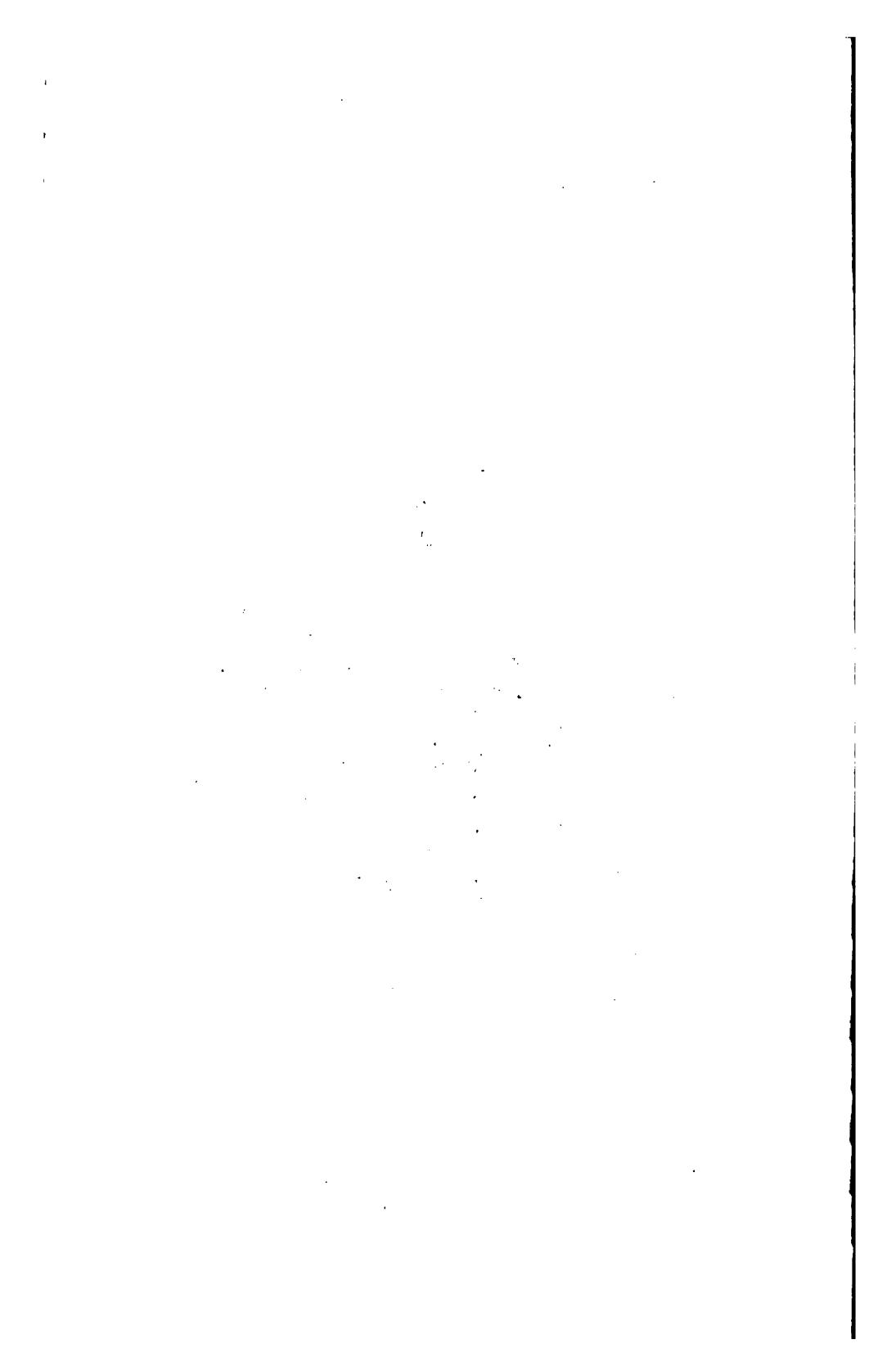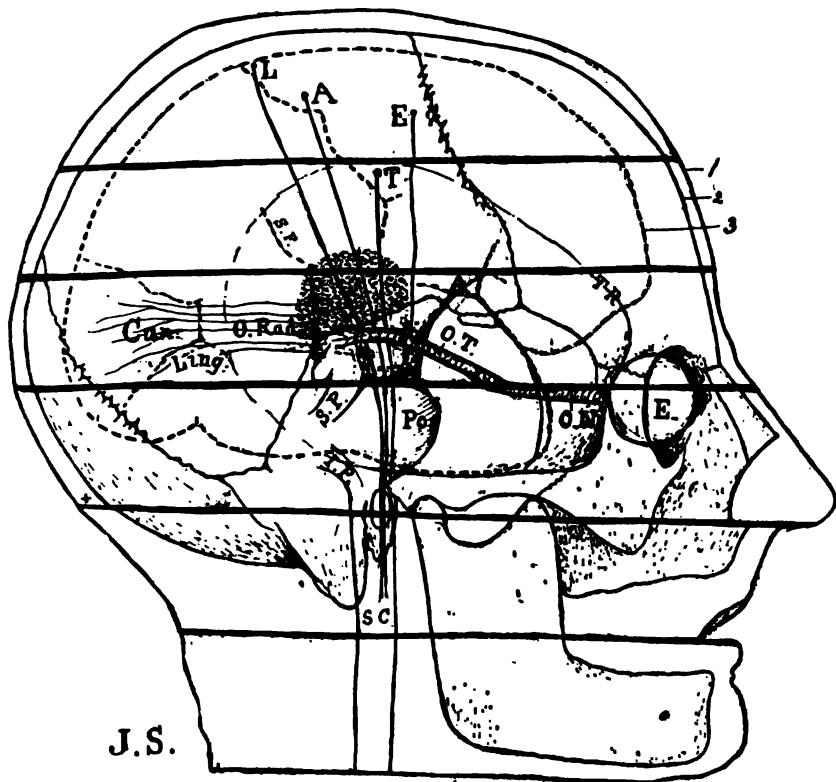
Plate VI.

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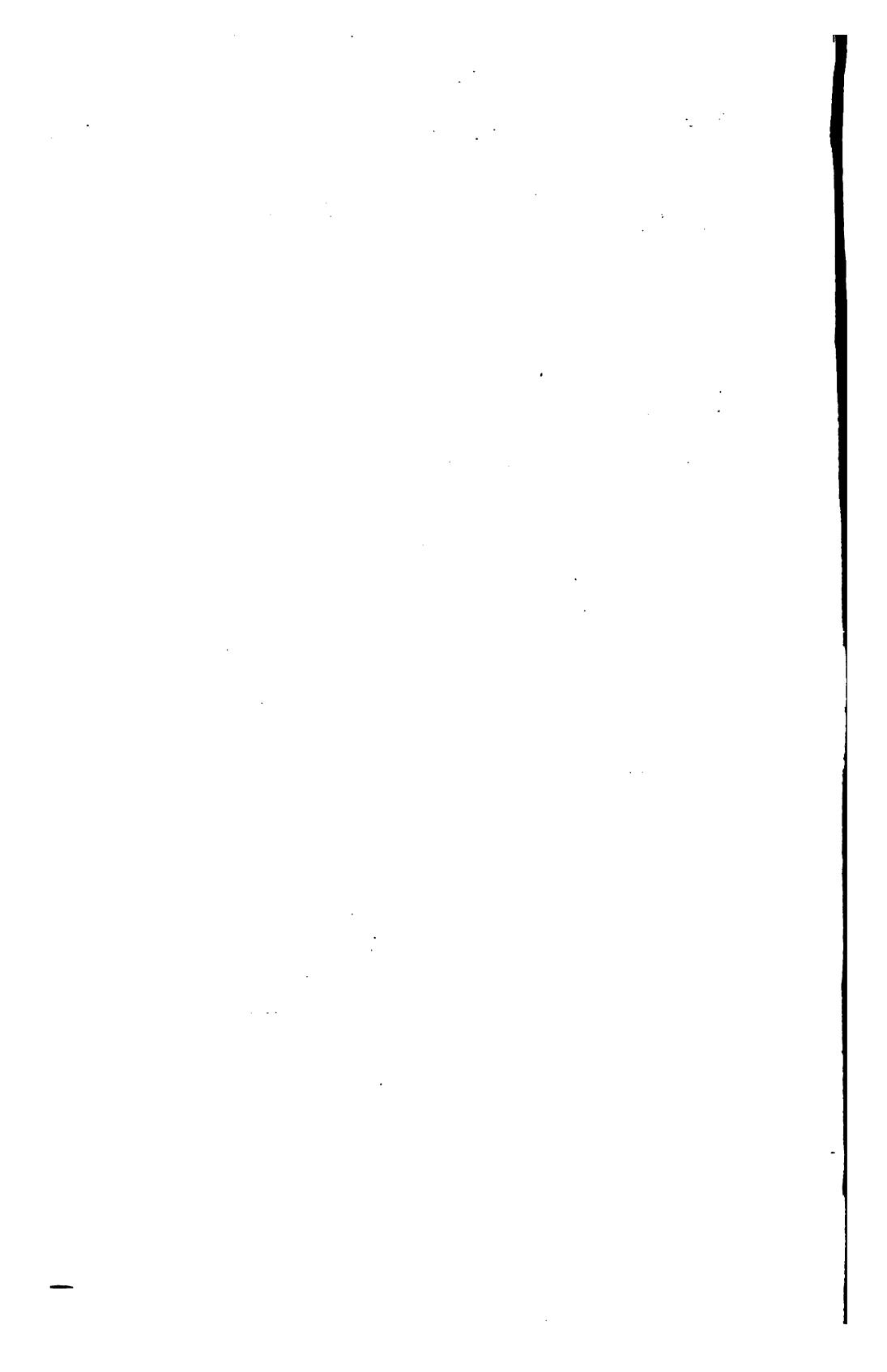
AN EXAMPLE OF A PECULIAR MALFORMATION OF THE TRICUSPID VALVE OF THE HEART. By T. WARDROP GRIFFITH, M.D., M.R.C.P., *Professor of Anatomy at the Yorkshire College ; Senior Assistant Physician to the General Infirmary, Leeds.* (PLATE XXX.)

THIS specimen came under my notice when I was making a post-mortem examination in the case of a little girl of the age of 5, who had died of cancrum oris. Before beginning the examination, I noticed that the finger-ends were clubbed to a slight but to an unmistakable extent, and this led me to express to the students who were present my suspicion that we should find either some congenital malformation of the heart, or some pleural or pulmonary disease of long standing. So far as could be ascertained, no cyanosis had been observed during life.

The heart was preserved in dilute spirit, and was not ex-amined in detail for some months. The organ weighed 1260 grs. The circumference of the aorta was $1\frac{7}{8}$ inches, that of the pulmonary artery $1\frac{3}{8}$, so that not only was there a reversal of the normal relationship as to circumference between these two vessels, but the difference in this case amounted to no less than half an inch.

The foramen ovale was widely patent, its valve small, reach-ing only about half-way across the aperture, and in part net-like. The continuity of the Eustachian valve with the Thebesian was very well marked, and was of such a kind that the coronary sinus opened into the same part of the auricle as the inferior vena cava. I may remark in passing that this peculiarity of the coronary sinus opening into the sinus venosus rather than into the auricle proper was also noticed by me in a specimen, shown at the meeting of the Anatomical Society held in 1896, of congenital cardiac malformation, with im-perfection of the interauricular septum, an absence almost complete of the ventricular septum, and non-differentiation of the two auriculo-ventricular openings from one another. In the discussion which followed, Prof. Thane made the interesting

observation that this manner of opening of the coronary sinus might be regarded as a persistence of the primitive arrangement, the coronary sinus opening, of course, in the first instance, into the sinus venosus, of which indeed it forms the left horn, and that the condition normally found in the adult must be due to some rearrangement, at present not fully understood.

Both auricles were capacious, possibly equally so; the left ventricle was disproportionately large and thick-walled as compared with the right.

Both flaps of the mitral valve showed an extreme degree of development of the thin net-like portion at the free margin, so that in the case of the anterior segment the measurement from the attached to the extreme free margin was two inches. The posterior segment was composed of at least two subsidiary flaps.

The aortic flaps were normal, and much more substantial than the pulmonary.

The right ventricle, as already remarked, was smaller than the left, and entered into the formation of the apex less than normally. Externally, it was noticed that just below the auriculo-ventricular furrow the part of the ventricular wall forming the margo acutus and the adjoining part of the anterior, and to a greater extent of the posterior, surface of the heart was very thin, and almost devoid of muscular tissue.

There was a very profound malformation of the tricuspid valve. The septal flap was quite isolated from the others, looking rather like an inverted semilunar segment, without distinct chordæ tendineæ, but having its usual relationship to the pars membranacea septi. The left or great flap was less fringed at its margins than normally, its upper commissure was fixed by confluent and rudimentary chordæ to the septum, quarter of an inch from the septal flap, while, when traced to the right, the ventricular aspect of this flap was found to be obscured by great columns of muscular tissue passing from the upper part of the ventricle downwards to the lower part of the anterior wall, and closely adherent to the valve. Between these columns, in some parts, the fibrous tissue of the valve was visible, and at two places small dome-like projections of

this fibrous tissue were seen, with apertures at their apices, whose margins were provided with chordæ tendineæ attached at the other end to the above noted muscular bands passing to the ventricular wall. It would appear from a careful replacement of the cardiac walls where these had been cut that the free margin of the anterior flap had been directed upwards and forwards to the pulmonary artery, and the whole of this free margin would correspond in a normal valve to that part of the flap extending from its apex to its junction with the septal flap. This margin bounded with the upper part of the septum and the septal flap of the tricuspid, a narrow strait through which most of the blood would pass on its way from the auricle to the ventricle. The rest of the margin of the great anterior segment was obscured by muscular bands as above described.

A probe passed from the pulmonary artery, therefore, could pass in two ways, viz., (1) along to the right into a gradually narrowing portion of the ventricle, which became blind at the margo acutus, and into which the two funnel-like apertures above mentioned opened, or (2) down between the anterior and septal flaps into another part of the ventricle.

The deformity of the posterior flap may best be understood by suggesting as a possible explanation of its condition, that it had been destroyed at its auriculo-ventricular attachment, and become adherent along its entire free margin with the ventricular wall, a condition associated with complete disappearance of the chordæ tendineæ and musculi papillares, and also associated with a large deficiency in the upper part of the flap and a smaller one nearer the septum.

From the right auricle, therefore, the blood might have passed (1) into the left auricle through the patent foramen ovale, or (2) through the auriculo-ventricular opening into the second part of the ventricle referred to above; here the blood would in the first instance pass in part behind the posterior segment of the tricuspid valve, and reach the main stream by sweeping above its upper margin or going through the deficiencies in its substance, whence it would pass directly to the conus arteriosus and pulmonary artery by going between the free margin of the tricuspid valve and the septum, and indirectly by going through

the two crater-like orifices described above as opening into the blind part of the ventricle, whence, of course, it would pass to the left and upwards to the pulmonary exit.

It is clear, therefore, that there must have been some slight obstruction to the passage of the blood through the right ventricle; and in harmony with this we note that the pulmonary artery was much smaller than the aorta.

A, in right auricle, points to crista terminalis.　Auricular septum and foramen ovale not shown.　*B*, isolated septal flap of tricuspid valve.　*C*, in second or blind part of right ventricle, points to the two crater-like orifices in the anterior tricuspid segment, which is here concealed by fleshy columns.

PROF. WARDROP GRIFFITH.

NOTE ON A SECOND EXAMPLE OF DIVISION OF THE CAVITY OF THE LEFT AURICLE INTO TWO COMPARTMENTS BY A FIBROUS BAND. By T. WARDROP GRIFFITH, M.D., M.R.C.P., *Professor of Anatomy, Yorkshire College, Leeds; Assistant Physician, General Infirmary, Leeds.* (PLATE XXXI.)

AT the meeting of the Anatomical Society held in February 1896, I showed a heart with a fibro-muscular band passing across the left auricle, which had the effect of partially dividing that cavity into two compartments,—an upper, receiving the pulmonary veins, and a lower, which, communicated with the ventricle and with the auricular appendix. I have recently met with another specimen presenting so many points of resemblance to the former that I think it should be put on record as well.

The heart was obtained at the post-mortem examination of a male patient who died at the age of 48 of chronic Bright's disease. The organ was much hypertrophied, and there were slight degenerative changes at the root of the aorta and in the mitral valve, which, however, appeared to have been competent.

The plate in illustration of this communication is from a photograph taken by Mr Michael Teale, one of our honorary demonstrators.

The left auricle was partially divided into two compartments by a broad fibrous band, which started from the auricular septum where it was continuous with the tissue of the valvula foraminis ovalis, from which it arose by several spurs. This band passed upwards and forwards below the upper right pulmonary vein, then along the anterior and left walls of the auricle, having now a downward direction, and passing just below and in front of the left pulmonary veins, and finally becoming narrower, was lost on the posterior wall of the auricle, about one inch above the auriculo-ventricular furrow. By its concave margin, which was well defined and smooth, it formed about three-fifths of the circumference of the aperture of communication between the two compartments of the auricle, the

remaining two-fifths being formed by the auricular wall at the posterior part of the septum and the adjacent part of the posterior wall. The aperture admitted of the passage of two fingers easily. Where the band was attached to the auricular wall, it presented several small deficiencies, through which a crow quill could be passed from the upper or posterior to the lower or anterior compartment of the auricle; these were situated towards the anterior and left part, where the band was thinner than elsewhere. Into the upper compartment of the auricle there opened the four pulmonary veins, the floor of the superior right and of both the left being directly continuous with the posterior or upper aspect of the band, while the inferior vein of the right side opened into the auricle some distance behind the origin of the band from the valve of the foramen ovale. The lower compartment of the auricle was in communication with the appendix, and, of course, with the ventricle through the mitral orifice. The foramen ovale was completely closed.

In commenting on my former specimen at the meeting of the Anatomical Society, I suggested as a possible, but as I said a highly problematical, explanation of the presence of the band, that there had been a failure in the complete amalgamation of that part of the auricle which is said to be formed from the confluent portions of the pulmonary veins and that derived from the left-hand division of the common auricle of the embryonic heart. This view did not meet with much acceptance at the meeting; and it was indeed advanced by me in a very tentative manner, and with no very strong conviction of its accuracy.

At the same meeting Dr Rolleston showed a band in the left auricle of a boy's heart, which was round and fibrous and crossed over the orifice of the mitral valve, but this was attached to the wall of the auricle *below* the appendix and *below* the level of the fossa ovalis. He also referred to Dr J. K. Fowler's specimen (*Path. Trans.*, 1882) of a band ¼-inch wide, with its edges vertical, which was attached to the septal wall, being here continuous with the membrane forming the fossa ovalis. This band was regarded by Dr Fowler as an overgrowth of the valvula foraminis ovalis, swept by the blood-

[PLATE XXXI.
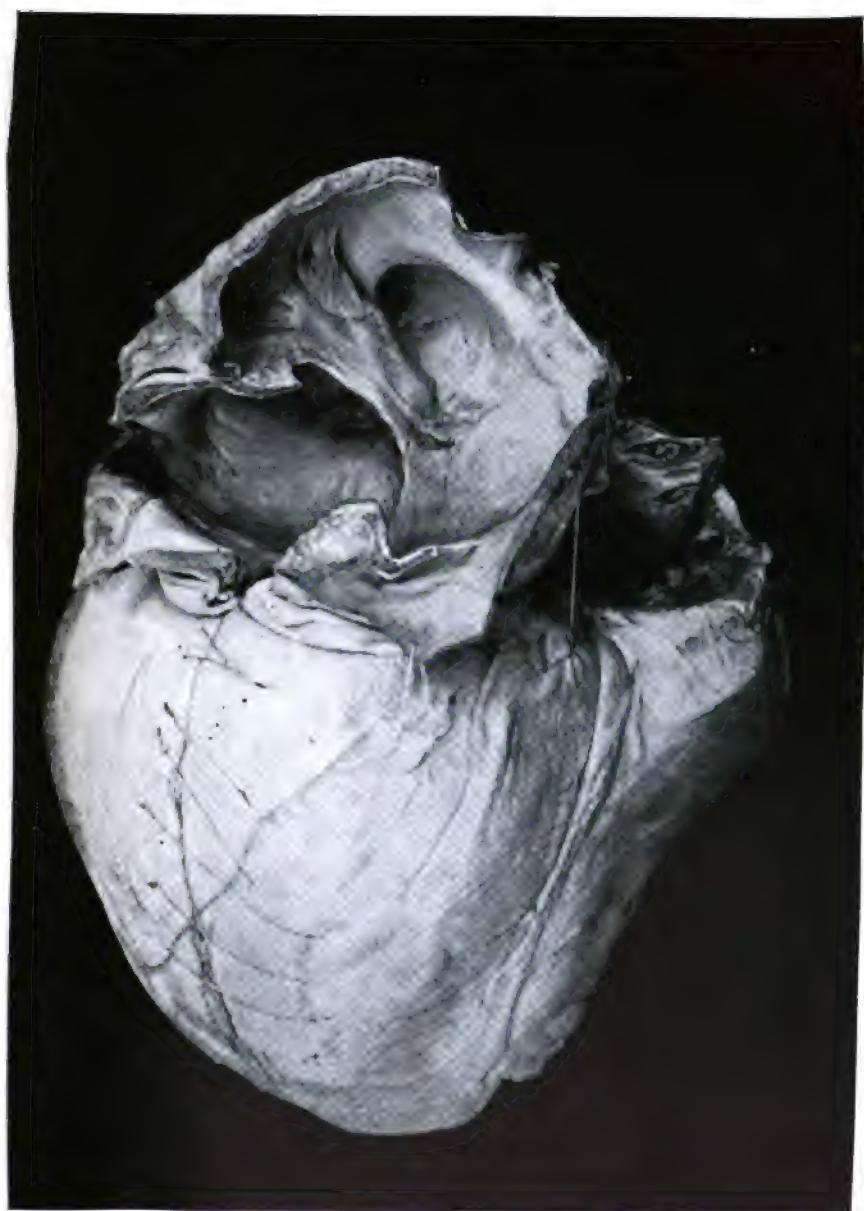
PROF. WARDROP GRIFFITH.
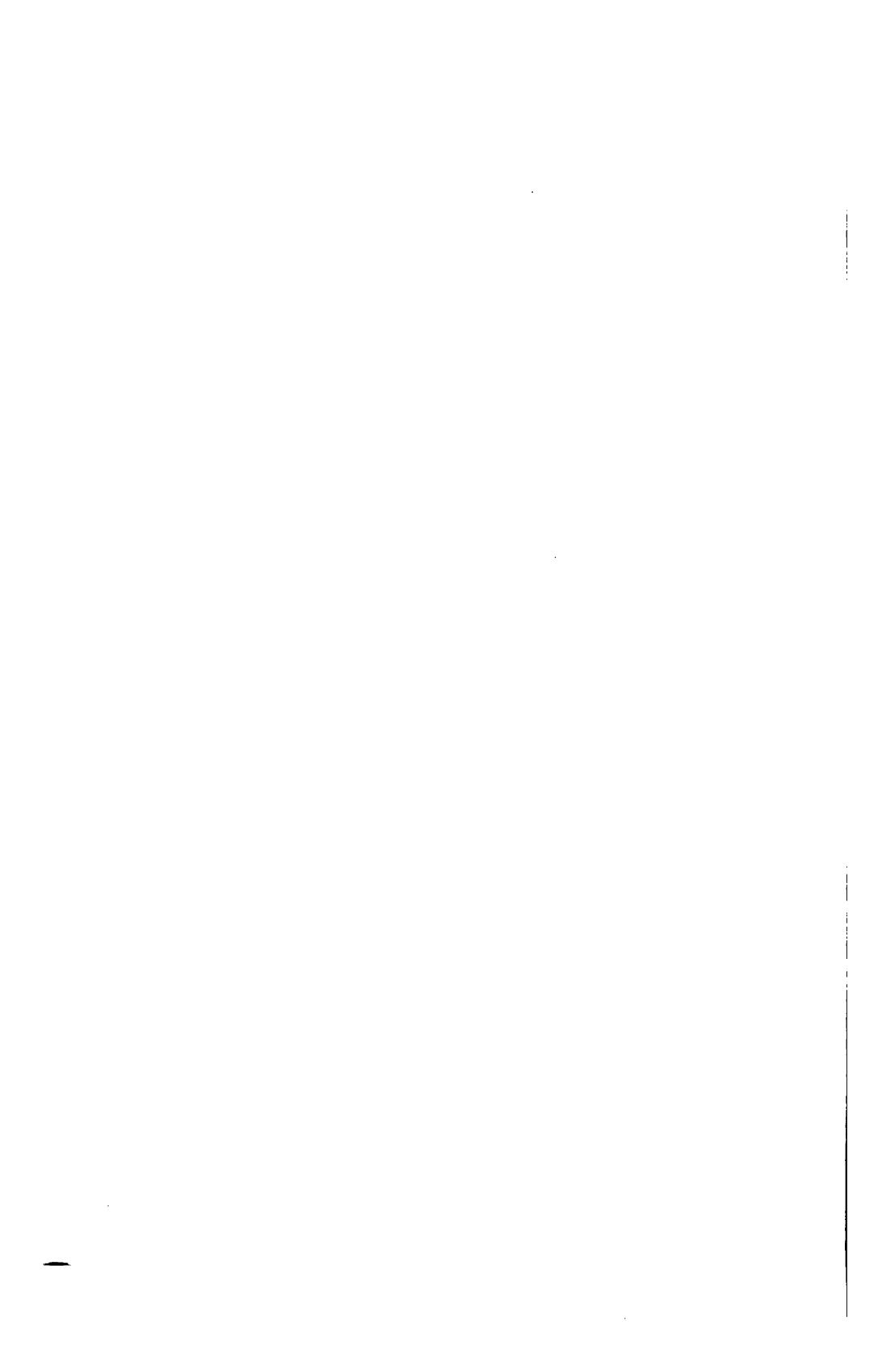
stream to the outer wall of the auricle, where it had become adherent.

In writing an account of my specimen, which I did after perusing the account of Dr Fowler's case, I came to the conclusion that he was correct in regarding the band as a redundancy of the tissue of the valve of the foramen ovale, and that my specimen was an example of the same thing; but I expressed my belief that in both cases we had to do with a mere exaggeration of a state of affairs not usually regarded as abnormal, viz., the presence of retinacula proceeding from the margins of the valve of the foramen ovale, which might or might not be patent.

At the meeting of the Society held at Cambridge in 1899, Professor Sidney Martin showed a specimen presenting a very strong resemblance to mine, and advanced the same explanation which I had, with great hesitation, given in 1896.   Dr Rolleston's specimen showed a rounded band, and its attachments were different.   I have not had the privilege of examining Dr Fowler's specimen, but his description would lead me to think it resembled my specimen rather than Dr Rolleston's; between my two specimens and Dr Sidney Martin's there is so strong a resemblance that I cannot regard the condition as in any way due to pathological causes, of which, indeed, there is no evidence, but I think it must depend on some such anomaly of development as has been suggested by Dr Martin and myself.   Perhaps, when the development of the pulmonary veins and their manner of junction with the left auricle is more fully understood, the explanation may become less uncertain.

THE CEREBRUM OF A MICROCEPHALIC IDIOT. By N. C. MACNAMARA, F.R.C.S., and R. H. BURNE, *Anatomical Assistant in the Museum of the Royal College of Surgeons of England.*

THE following notes have been kindly sent to us by Dr F. Pritchard Davies.

F. W. B. was admitted into the Kent County Asylum in December 1886. He remained in that institution until his death, which took place when he had reached the age of twenty-two years. He was 4 feet 8½ inches in height; his features are stated to have been " large and coarse (fig. 1), and devoid of expression; his arms were better developed than his body, head, or legs, giving him a simian appearance. His cranial development was of a low type; the occipital bones had fused early, and the size of the cerebrum was insignificant."

The report further states that F. W. B. " was unable to speak, but expressed his wants and such ideas as his mind could formulate by signs and inarticulate noises. He was entirely devoid of intelligence, but seemed to appreciate the sound of musical instruments. He had to be constantly under super-vision, as he was mischievous and dirty in his habits. F. W. B. was very passionate, and when out of temper became violent, throwing himself on the ground, uttering loud inarticulate sounds, and beating his chest and face with his hands until his mouth and nose bled." His eyesight and sense of smell and hearing were good. When twenty-two years of age he developed phthisis, and died somewhat suddenly.

From notes taken at the time of the post-mortem examination of F. W. B.'s body, we learn that " from the glabella to the occipital protuberance his skull measured 7½ inches, and from the tip of one mastoid process to the other 8¼ inches. The circumference of the cranium round the line of the occipital protuberance and frontal eminences measured 14¼ inches." No other measurements of the skull are recorded. The brain weighed 12¼ ounces; " the cerebellum projected ¾ of an inch

beyond the occipital lobe." The brain had been preserved in spirit for some years before it came into our possession. At the time of making the post-mortem, the saw had cut into the surface of the cerebrum, and to some extent damaged the specimen, as shown in fig. 3.

This specimen is now in the Museum of the Royal College of Surgeons of England (No. D. 683, Physiol. Series). From a

FIG. 1.

photograph taken of its vertex, it will be seen that the cerebral hemispheres do not by any means cover the cerebellum (fig. 2). The remarkably small size of this adult human brain, and the defective development of its frontal opercula, and of its parietal and occipital lobes, are its most striking features.

In F. W. B.'s cerebrum the stem of the Sylvian fissures in both hemispheres and their posterior horizontal limbs are alone present. The posterior ramus of this sulcus on the right side

is nearly at a right angle with the long axis of the cerebrum; on the left side it has an angle of about 65°.

In the left hemisphere the orbital and frontal opercula are wanting, and the fronto-parietal operculum is imperfectly de-

Fig. 2.—View of the brain of F. W. B. as seen from above.

veloped, the insula being only partially covered by the temporal operculum (fig. 3). In the right hemisphere this condition of the opercula was marked, but in order to expose the whole of the island of Reil on this side, portions of the frontal and temporal lobes have been removed (fig. 4). It will be seen that

the insula in F. W. B.'s brain consists of a small smooth nodule; it has no gyri or sulci on its surface, unless the depression on its lower and anterior part may be taken to be a rudimentary longitudinal fissure. The fronto-orbital sulcus is well defined; commencing on the orbital surface of the frontal lobe and bending round the lateral margin of the hemisphere, it ascends for a short distance on its outer surface. This sulcus, as Professor D. J. Cunningham has demonstrated, forms the anterior limiting sulcus of the island of Reil in the anthropoid
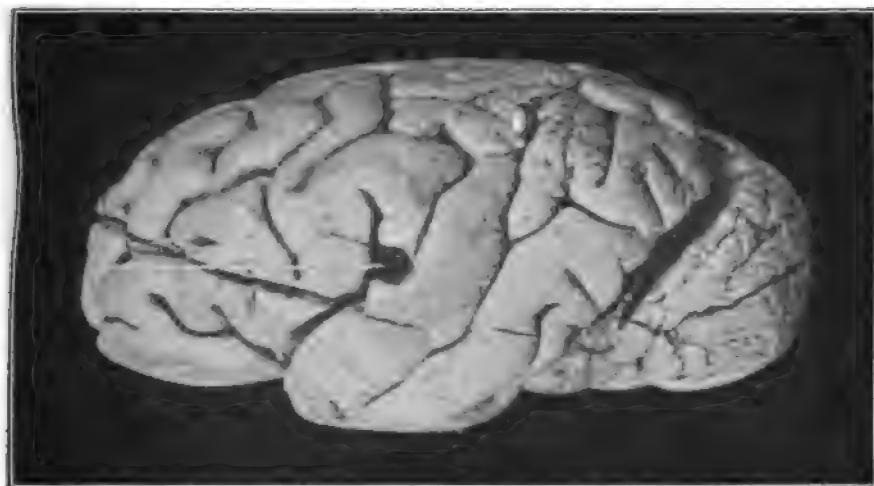
FIG. 8.—Left profile view of the brain of F. W. B.

apes; it also clearly bears this relation to the insula in the case of F. W. B.'s cerebrum (fig. 4).

If we compare the conformation of the surface and the size of the island of Reil in F. W. B.'s cerebrum with that of a full grown chimpanzee or of an adult human being (fig. 5 and fig. 6), it will be seen how extremely ill-developed the insula is in the case of this idiot.

Professor D. J. Cunningham has described and given excellent drawings of two microcephalic brains, which in the anatomical relation of the parts forming the Sylvian and insular region are almost identical with that of F. W. B.'s cerebrum.[1] The same

[1] *The Scient. Trans. of the Royal Dublin Society,* vol. v. (series ii.) p. 287, 1895.

remark applies to the fissure of Rolando, which on the right side of F. W. B.'s brain does not reach the supero-mesial border of the hemisphere; on the left side it bifurcates before reaching this border. This sulcus is shallow and has smooth walls; it bifurcates at its lower extremity in both hemispheres.

On the right and left side of this brain the superior and inferior præcentral sulci form continuous fissures; from their lower part sulci pass into the gyrus frontalis medius. The superior frontal sulci on both sides are broken up into shallow furrows, and it is
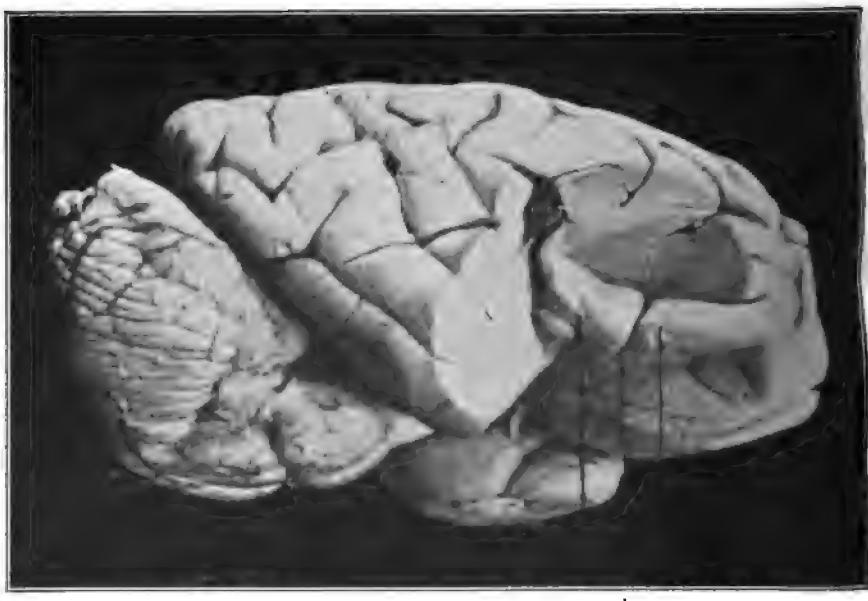
FIG. 4.—Right profile view of the brain of F. W. B. The fronto-parietal and the temporal opercula have been removed. *a*, island of Reil; *b*, fronto-orbital sulcus; *c*, 3rd frontal gyrus.

difficult to define the middle from the superior gyrus. The lower frontal gyri, as already stated, are defective as regards their opercula, and are altogether ape-like in their conformation.

It is, however, in that part of the cerebrum which lies posterior to the central sulcus that the most marked anomalies are noticeable in F. W. B.'s cerebrum. The calloso-marginal sulci cut into the superior borders of the hemisphere, posterior

to the upper end of the central fissure. The intraparietal sulci in both hemispheres are of an ape-like character, and form continuous fissures which pass diagonally across the parietal lobes.

The parieto-occipital sulci on the lateral surface of the hemispheres, especially on the left side, pass into fissures which correspond to that of the 'affenspalte' of the ape's cerebrum,
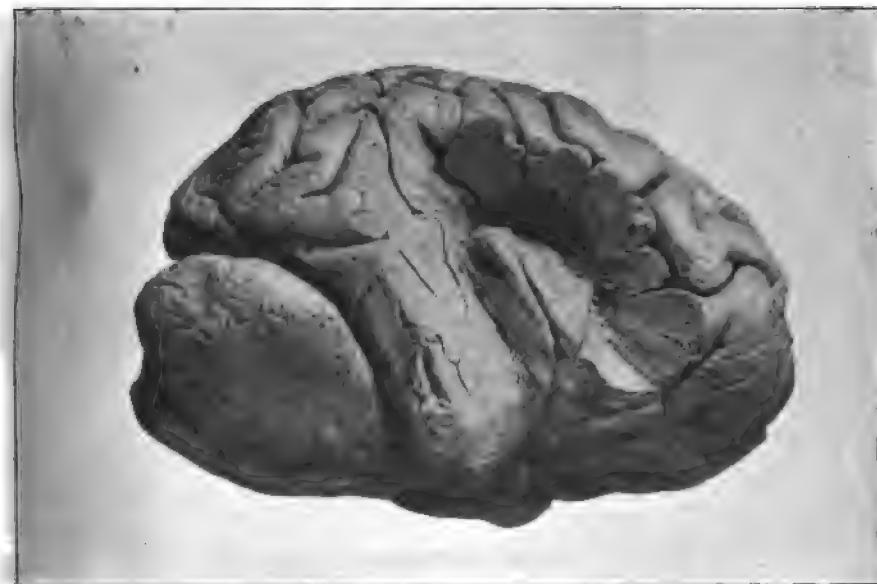
FIG. 5.—Brain of chimpanzee. The opercula have been removed to expose the insula.

but there is no occipital operculum, although these sulci are crossed by one if not two deep annectant gyri. On the mesial surface of F. W. B.'s cerebrum we find that the occipito-parietal sulci are short, and in both hemispheres are separated from the calcarine fissures by a superficial gyrus cunei. The calcarine sulcus forms a deep fissure, extending from the hippocampal sulcus to the posterior margin of the abortive occipital lobe; it is throughout its length on the tentorial surface of the cerebrum. External to the calcarine, the collateral sulcus extends forward to near the anterior border of the temporal lobe. The calloso-

marginal sulcus on the left side forms a well marked continuous fissure; on the right side, the posterior and median portion of this sulcus are united, the anterior part forming a separate fissure.

The temporal lobes project but slightly beyond the inferior terminal portion of the great limbic lobe. In both lobes the first and second sulci are clearly defined, but the third fissure can hardly be said to exist.

FIG. 6.—Normal human brain. The opercula have been removed to expose the insula.

It is unnecessary for us to enter on a more detailed account of this brain, for, as we have already remarked, its anatomical characters closely resemble those so ably and fully described by Professor Cunningham. But so far as the structure of F. W. B.'s cerebrum is concerned, it is clear that it differs less from the brain of anthropoid apes than it does from the cerebrum of a normal adult human being. We may go beyond this, and state that the brain of this microcephalic idiot in its anatomical characters is more closely allied to that of an adult male chim-

panzee than it is to a human cerebrum at any stage of its development.

Although more than one brain centre is concerned in the faculty of speech, it is certain that the region of the cerebrum, which is formed by the opercula of the third frontal gyrus of the left hemisphere, has a direct influence over man's characteristic power of intelligent language. In the case of F. W. B. these opercula can hardly be said to exist, and the insula is only present in a rudimentary form. This point is more forcibly demonstrated by reference to the photographs (figs. 4, 5 and 6) than by any written description we can give. But from other microcephalic brains in our possession, this almost total want of development of the insula is by no means so constant a character of these cerebral hemispheres as is that of their defective frontal opercula.

It is useless to dilate on the interest which the histories of the cases above referred to possess in connection with the anatomical characters presented by these brains. It is much to be desired that series of such histories and brains should be brought together in our large museums, so that they might be carefully studied and compared with one another. They should comprise "brains in which no pathological taint can be discovered, and which present certain common morphological features, and a certain more or less easily distinguished uniformity of type."[1]

[1] *Sci. Trans. Roy. Dub. Soc.*, vol. v., 1895, p. 289.

A DESCRIPTION OF SOME ANOMALIES IN NERVES ARISING FROM THE LUMBAR PLEXUS OF A FŒTUS, AND OF THE BILAMINAR MUSCULUS PECTINEUS FOUND IN THE SAME FŒTUS; WITH A STUDY OF THE VARIATIONS AND RELATION TO NERVE SUPPLY IN MAN AND SOME OTHER MAMMALS.[1] By Edward B. Jamieson, M.B., Ch.B., University of Edinburgh.

ONE of the chief points of interest in connection with the anomalies given in the following description is that they have all been found in one subject. Similar or identical irregularities, occurring usually singly, have been described before; but it is uncommon to find in one subject an aggregation of anomalies which do not stand related to one another. In extreme forms of lumbar plexus, of either high or low type, one expects to find correlated variations in the origin of nerves; and when a number of nerves have peculiarities in origin, it is usually due to the form of the plexus. In the case hereinafter described, however, the plexus was of ordinary type, and the two principal nerves—the Anterior Crural and the Obturator—were formed in the usual manner. The peculiarities affected certain of the smaller nerves—the Ilio-hypogastric, and the External and Middle cutaneous nerves of the thigh; and besides, there were found nerves which do not commonly exist—two Accessory Obturator nerves, and one which might be called the Accessory Anterior Crural nerve. Moreover, these irregularities were not symmetrical; the only feature in those irregularities which the plexuses of the two sides had in common was the presence of an Accessory Obturator nerve on each side.

The bilaminar Pectineus in this case is of interest, firstly, in that it was present along with an Accessory Obturator nerve, and yet received no branch from it; and secondly, in that it

was found in a fœtus (female, 5½ months).   The study of most abnormalities in a fœtus is of value as a means of throwing light on the problems of adult structure, and many such problems are elucidated only by the study of the arrangements of fœtal structure, as that is still undergoing development; and the advantages increase when, in a fœtus, a condition is found akin to the occasional anomalous conditions found in the adult. In the case of muscles, it may not only be as yet in a developmental stage, especially in those examples where there is a tendency to show a compound character, but the conditions, also, may be different owing to the absence of any modifying influences which action may bring to bear upon it.

The Lumbar Plexus.

The two plexuses were of ordinary type, and were alike, except that an extra communicating loop passed from the Second to the Third nerve on the left side, and that the First nerve on the right side was smaller than that on the left.   On neither side was there a communicating loop from the Twelfth Thoracic to the First Lumbar nerve.

The Ilio-hypogastric Nerve.

On the right side, this nerve was given off from the Twelfth Thoracic.   The Twelfth Thoracic nerve was larger than that of the left side.   It gave off two iliac branches, and divided into two branches which ran along the anterior abdominal wall. The lower branch corresponded to the Ilio-hypogastric nerve. The upper branch was the Twelfth Thoracic proper.

The Ilio-hypogastric nerve coming off in common with the last Thoracic is not unusual.   Schmidt (1, a) described this arrangement in one out of three or four bodies.   In such a case the Ilio-inguinal was larger than usual.   It may come not only from the Last Thoracic, but may also get a small root from the Eleventh Thoracic (Quain, 2, a).   There may be certain degrees of reciprocal development between the Last Thoracic and the Ilio-hypogastric nerves, so that when the one is large the other is small or absent (Macalister, 3, a).

THE ACCESSORY ANTERIOR CRURAL NERVE.

When the anterior surface of the Psoas muscle of the right side was exposed, two nerves were seen lying on its surface. The internal nerve was the Genito-crural. The external, a much larger nerve, ran down on the surface of the Psoas, crossing obliquely outwards to join the Anterior Crural nerve a short distance above Poupart's ligament. Some of its fibres entered into the substance of that nerve, but the bulk of it was merely bound down to the Anterior Crural by the fibrous tissue of the nerve-sheath. The lower limb of the right side had been removed some time before this dissection was commenced, and this nerve could not be traced beyond Poupart's ligament. On tracing it back through the Psoas to its origin, it was seen to be formed by two pieces, of which the upper and more slender piece arose from the Second Lumbar nerve shortly after it had been joined by the communicating branch from the First; the lower, larger piece, from the Second nerve at its junction with the root of the Anterior Crural from the Third nerve. The two pieces came forwards independently through the substance of the Psoas, and united as soon as they reached its anterior surface.

Winslow (4, a) described a nerve similar to this, but with a slightly different origin, and he called it an accessory or companion nerve to the Anterior Crural ("*On le peut regarder commé L'Accessoire ou L'Associé du Nerf Crural*"). It was given off by the Third Lumbar nerve, ran down between the Iliacus and the Psoas, and joined with the Anterior Crural nerve to the outer side of the Psoas. Schmidt (1, b) described the plexus of Martin and Gunther, which he found twice in seven bodies. One of the two varieties of this plexus, which he mentioned, is similar to the nerve I have described:—A considerable branch came from the union of the communicating loops of the first three Lumbar nerves before the Third joins the Fourth, and lower down united with the Anterior Crural. Schmidt also mentioned a branch described by Vieussens (1, c), which sprang from the Third Lumbar nerve and joined the Anterior Crural in two pieces. In each of these three cases there is a certain similarity to the nerve I have described, but in none of them is there the

precise mode of origin, nor does any of them bear the same relation to Psoas.

THE MIDDLE AND EXTERNAL CUTANEOUS NERVES.

On the left side there was no separate, distinct External Cutaneous nerve. Both External and Middle Cutaneous nerves were given off directly from the Second Lumbar by a number of roots, which combined in the substance of the Psoas to form three nerves. These pierced the Psoas and lay on its anterior surface, so that when this muscle was exposed five nerves were seen lying on its surface, the two most internal being the two divisions of the Genito-crural nerve. The three nerves ran down over the Psoas, inclining to its outer side, till they lay on the Anterior Crural nerve behind Poupart's ligament. Through-out their course they communicated with each other by many very fine nerve-filaments. Behind Poupart's ligament the outermost nerve divided into an outer, larger branch, which took the place of the posterior division of the External Cutaneous, and an inner branch which joined the middle nerve. The nerve formed by this union represented the outer branch of the Middle Cutaneous. The innermost nerve divided above Poupart's ligament into two equal branches. The outer supplied the place of the anterior division of the External Cutaneous, the inner represented the inner branch of the Middle Cutaneous.

An arrangement of the External and Middle Cutaneous nerves of the thigh precisely like the foregoing I do not find recorded, but, at different times, arrangements bearing some resemblance have been met with. Winslow (4, b) described two nerves which arose from the Second Lumbar nerve, and having pierced Psoas at different places, ran downwards and passed out under the upper part of the Fallopian ligament, uniting as they did so to form one nerve. This nerve divided into branches which were distributed to inguinal glands, to crural aponeurosis, and to the front of the thigh as far as the knee. Some united with branches of the Anterior Crural; others went to the inner side of the thigh; one accompanied the Crural artery.

Schmidt (1, d) described various communications between the Middle and External Cutaneous nerves, and instances of these

nerves arising in the abdomen :—He had seen the Middle
Cutaneous springing from the second ansa of communication,
and had seen it joining a branch of the External Cutaneous. He
had also seen the External Cutaneous sending a branch to join
the Middle Cutaneous. He had further observed the Anterior
Cutaneous, *i.e.* the inner division of the Middle Cutaneous,
arising from the ansa of the Third pair; piercing the Psoas, it
ran down over it, and passed under Poupart's ligament to be
distributed to the thigh. The External Cutaneous nerve
frequently accompanies, or is united with, the Anterior Crural
nerve to below Poupart's ligament (Quain, 2, *b*); this was also
seen by Schmidt twice in about thirty cases. The posterior
branch of the External Cutaneous may be replaced by a branch
from the Genito-crural nerve (Quain, 2, *b*).

The Accessory Obturator Nerve.

Origin.—An Accessory Obturator nerve was found on the
left side arising from the Third Lumbar nerve. Its apparent
origin was from the angle between the roots to the Anterior
Crural nerve and the Obturator; but having been traced back-
wards, it was found to turn round behind and below the
Obturator part of the nerve, and to arise from the front and
inner side of that portion; and all its fibres came from this
Obturator portion.

Course.—It ran downwards behind Psoas towards the pelvic
brim, and then along the pelvic brim behind the Inner border
of Psoas, external to the Obturator nerve. It crossed the
public ramus in close contact with the inner border of the
Psoas behind the external iliac vein, and passed behind the
Pectineus and afterwards the Adductor Longus. Lying there
in front of Obturator Externus and Adductor Brevis, it had the
anterior division of the Obturator nerve to its inner side, and
was crossed, anteriorly, by the branch of that nerve to the
Adductor Longus. It appeared at the inner border of the
Adductor Longus about its middle, and continued downwards
along the inner border of the Adductor Longus until that
muscle was crossed by the Sartorius. Thence it passed under
cover of Sartorius, and crossed obliquely in front of the lower

and inner part of the fibrous roof of Hunter's canal. The Long
Saphenous nerve, immediately after its emergence from under-
neath the fibrous roof of Hunter's canal, crossed in front of it
as it lay under Sartorius. It appeared at the anterior border
of the Sartorius at the level of the adductor tubercle, and
having pierced the deep fascia, it ran forwards and downwards
in the superficial fascia towards the patella.

Branches.—While it lay on the Os Pubis it gave off a branch
which passed directly outwards, to end in the capsule of the
hip-joint behind Psoas. While it lay behind Pectineus, and in
front of Obturator Externus, it gave off one small branch which
passed directly backwards, crossing the anterior division of the
Obturator nerve externally, to join the posterior division of the
Obturator nerve. This branch was traced to the Adductor
Magnus. A little below it gave off another small branch which
passed backwards, crossing the branches from the Obturator
nerve to the Adductors Longus and Gracilis and the Obturator
branch to the Pectineus, on their outer side, and joined the
branch from the anterior division of the Obturator nerve to the
Adductor Brevis. While it lay behind the Pectineus, and in
front of the Adductor Brevis, it gave off an exceedingly slender
branch which passed inwards behind the nerve to the Adductor
Longus, and joined the nerve to the Gracilis. While it lay
along the inner border of the Adductor Longus, two very slender
branches were given off close together, which passed forwards,
and having appeared at the anterior border of the Gracilis,
united with a branch of the inner (or posterior) division of the
Internal Cutaneous branch of the Anterior Crural nerve. While
it lay under cover of the Sartorius, a slender branch from it
passed downwards and backwards to unite with the inner
division of the Internal Cutaneous at the posterior border of
the Sartorius; several delicate filaments passed between it and
the Long Saphenous nerve; and one filament was given off and
passed downwards to end in the femoral artery as it passed
through the opening in the Adductor Magnus. The terminal
filament, in front of the Sartorius, was exceedingly fine; but it
could be traced forwards to the inner side of the patella, where
it divided into two branches, the upper of which passed directly
outwards over the patella, while the lower passed downwards

and outwards along the border of the patella. It supplied no branch, directly or indirectly, to the Adductor Longus, and none to the Pectineus. No cutaneous branch was given off by the Obturator nerve.

An accessory Obturator nerve of the same dimensions, but with a slightly different origin, was found on the right side. It was formed by two roots, both connected with the Obturator nerve. The main root came from the Third Lumbar nerve, out of the midst of the root of that nerve to the Obturator; this was joined by a small filament from the Obturator root from the Second nerve, as it crossed the Third nerve. It followed the same course as the Accessory Obturator on the left side. Owing to the previous removal of the lower limb of the right side all the distribution could not be followed, but sufficient had been left to show a branch given off to the front of the capsule of the hip-joint, a small communicating twig to the posterior division of the Obturator nerve, a larger communication to one of the branches of the anterior division of the Obturator nerve, and the cut end of what remained of the nerve.

RÉSUMÉ OF PREVIOUS DESCRIPTIONS OF THE ACCESSORY OBTURATOR NERVE.

Frequency.—Schmidt (1), who claimed to have been the first to mention and describe the Accessory Obturator nerve (§ xl.: "*Nervus quidam, hucusque nemini notus*"; and § xxix.: "*Nec non nervum ante me à nemine descriptum, utpote N. ad nervum cruralem internum, seu obturatorium, accessorium*"), found it four or five times in nine or ten bodies. Eisler (5) found it in 29 per cent. of cases. Paterson (6), out of twenty cases, found it in three.

Origin.—In its origin the nerve shows no constancy, but its variations are within certain limits. It is commonly described as arising from the Third and Fourth Lumbar nerves, in association with the roots of the Anterior Crural given off by these nerves (Quain, 2, *c*; Gray, 7). In the cases described by Paterson, it sprang from the Third nerve in association with the root of the Anterior Crural nerve. An occasional origin from only the Third Lumbar nerve is mentioned in Quain (2, *c*). It

may arise from the Fifth Lumbar nerve as well as from the Third and Fourth (Quain, 2, c). It may be given off from the trunk of the Obturator nerve (Ellis, 8). It is represented in three of the figures appended to Schmidt's commentary (1), and in each it has a different origin. In Table I. fig. 4 it comes out of a plexiform arrangement of the roots of the Obturator from the Third and Fourth Lumbar nerves; in fig. 5, it comes from the root to the Anterior Crural from the Third Lumbar nerve, and, by a slight communication, from the root to the same nerve from the Fourth, and also from the root from the Third Lumbar nerve to the Obturator. In Table II. it arises from the Third and Fourth Lumbar nerves before the Obturator and Anterior Crural nerve-roots have been given off.

Distribution.—In its distribution the Accessory Obturator nerve is very erratic, ranging from a minimal distribution to one structure to an extensive supply of muscles and skin of the inner side of the thigh. In the majority of instances it is distributed to the hip-joint, the Pectineus, and, by a communicating branch, to the superficial division of the Obturator nerve. When small, it may expend itself on the capsule of the hip-joint (Gray, 7, a), or it may supply nothing beyond the Pectineus; this supply may be complementary to the branch to the Pectineus from the Anterior Crural, or it may replace that branch (Paterson, 6, 9). When slightly larger, it supplies a branch to the hip-joint and a communicating branch to the Obturator nerve (Schmidt, 1, e). A still larger nerve gives the usual three branches. The communicating branch to the Obturator may, when traced out, be found to furnish supply to the Adductor Brevis, the Adductor Longus, the Gracilis, and, rarely, a cutaneous branch to the inner side of the thigh (Quain, 2, c). The most extensive distribution I find recorded was described by Paterson (10) in the case of a Negro, where an Accessory Obturator nerve was found. It arose from the Third Lumbar nerve, and gave branches as follows:—(1) to the Pectineus; (2) to join the nerve to the Gracilis; (3) to join the nerve to the Adductor Brevis; (4) to join the cutaneous branch of the Obturator, and through that, communicated with the internal cutaneous branch of the Anterior Crural and with the Long Saphenous nerve; (5) to the hip-joint; (6) to join the

posterior division of the Obturator, and through that, supplied branches to the Obturator Externus, to the Adductor Magnus, and to the knee-joint. The distribution of this nerve compares very closely with that of the one I have described, the differences consisting in that in this nerve it gave branches to the Pectineus, to the Obturator Externus, and to the knee-joint, and gave no branch to the femoral artery; and it gave only a contribution to
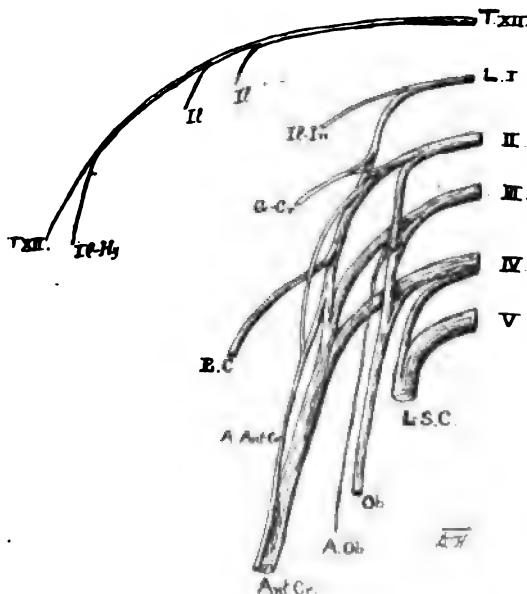
Fig. 1.—Right side. *T.xii.*, the last thoracic nerve. *L.I.* to *V.*, the lumbar nerves. *Il.,Il.*, the iliac branches of the last thoracic and the ilio-hypogastric nerves. *Il.-Hy.*, the ilio-hypogastric nerve coming off the last thoracic. *Il.-In.*, the ilio-inguinal nerve. *G.-Cr.*, the genito-crural nerve. *E.C.*, the external cutaneous nerve of the thigh. *A.Ant.Cr.*, the accessory anterior crural nerve. *Ant.Cr.*, the anterior crural nerve. *A.Ob.*, the accessory obturator nerve. *Ob.*, the obturator nerve. *L.S.C.*, the lumbosacral cord.

the cutaneous branch of the Obturator nerve, whereas, in the case I have described, the cutaneous nerve was wholly from the Accessory Obturator.

Paterson (6) has shown that the Accessory Obturator nerve, with three branches as commonly found, would be better named the Accessory Anterior Crural, on account of its origin and distribution. But in instances where the nerve is given off from

the roots of the Obturator nerve, or takes on a supply which is generally to be referred to the Obturator, this name is inapplicable.   There are, at least, three forms of so-called Accessory Obturator nerve, all passing over the pubic ramus internal to the Psoas:—1. The suprapubic nerve, large or small, which keeps
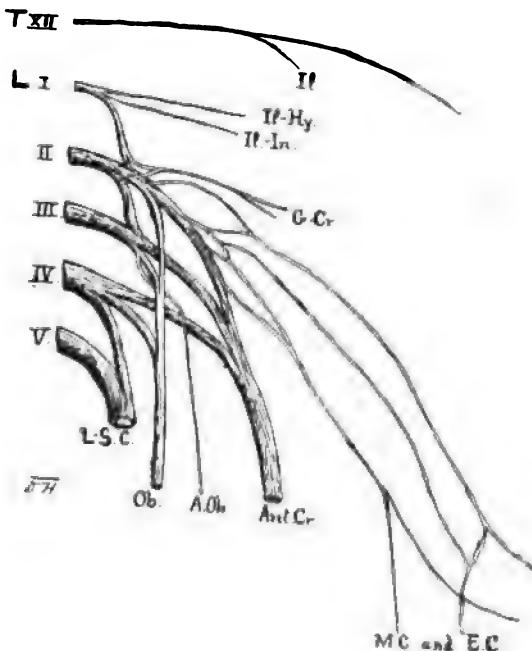
Fig. 2.—Left side. *T.xii.*, the last thoracic nerve. *L.I.* to *V.*, the lumbar nerves. *Il.*, the iliac branch of the last thoracic nerve. *Il.-Hy.*, the ilio-hypogastric nerve. *Il.-In.*, the ilio-inguinal nerve. *G.-Cr.*, the genito-crural nerve dividing into its genital and crural branches. *E.C.* and *M.C.*, the external and middle cutaneous nerves of the thigh : the two terminal branches nearest mid-line representing the middle cutaneous; the two terminal branches furthest out representing the external cutaneous. *Ant.Cr.*, the anterior crural nerve. *A.Ob.*, the accessory obturator nerve. *Ob.*, the obturator nerve. *L.S.C.*, the lumbo-sacral cord. [Figures 1 and 2 were drawn for me by Dr Hepburn.]

within the limits of the Obturator nerve distribution.   2. The suprapubic nerve, for which Paterson has suggested the name Accessory Anterior Crural.   3. The suprapubic nerve, consisting of the nerve to the Pectineus and part of the Internal Cutaneous branch of the Anterior Crural nerve, which, according to

Macalister (3), is misnamed Accessory Obturator. I doubt if any single, yet sufficiently comprehensive, name could be devised to include all of these; and a multiplication of names for an inconstant nerve to indicate all its vagaries would be of questionable advantage. The term Accessory Obturator nerve may, strictly speaking, be insufficient or incorrect; but, by convention, what is understood by that term is an inconstant nerve, with an origin varying within limits, which passes over the horizontal ramus of the pubis internal to the Psoas, and has a varying distribution in association with the Anterior Crural, or the Obturator nerve, or both; and a changing of its name into one which is not more comprehensive is unnecessary.

The Sacral Plexus.

This plexus, on both sides, both in its formation and in the nerves given off from it, was conspicuously normal.

The Bilaminar Musculus Pectineus.

Description.—The Pectineus consisted of two separate laminæ, an anterior or superficial and a posterior or deep. The anterior lamina took origin by fleshy fibres from the pectineal line and the surface of the horizontal ramus of the pubis below. It was of equal breadth throughout; towards the insertion it became tendinous, and was inserted into the posterior surface of the shaft of the femur behind the lesser trochanter, and into the upper part of the line leading down from the lesser trochanter towards the linea aspera. The posterior lamina was less thick than the anterior, and was narrower, especially at the origin, but it was fleshy throughout. It took origin from the front of the body of the pubis, immediately below the crest, and external to the Adductor Longus, and from a small part of the adjoining anterior surface of the horizontal ramus subjacent to the anterior lamella. From its origin it passed downwards, outwards and backwards behind the anterior lamina, to be inserted into the line leading down from the lesser trochanter, but falling short of the lower limit of attachment of the anterior lamina. As the inner border of the posterior lamina projected inwards beyond the anterior lamina at the origin, and the anterior

projected beyond the posterior at the insertion, the fibres of the anterior lamina crossed those of the posterior at an acute angle. The Adductor Longus was very closely adjacent to the posterior lamina at the origin and for some little distance beyond, but towards the insertion it was separated by a considerable interval from both laminæ.

Digest of previous descriptions of variations in the Pectineus.— Although the Pectineus presents, as a rule, no peculiarity, yet it is subject to frequent variations, and those of different kinds. Two forms of variation have been described which affect only itself, and other variations have been described which implicate neighbouring muscles, commonly those of the Adductor group.

Variations affecting itself are those in which the Pectineus is found divided, completely or incompletely, into two, and the splitting as described by Testut (11) may be in a direction such as to produce either two pieces lying side by side on the same level, or two laminæ or strata, one placed in front of the other. The latter condition seems to be the more common variation; and in Henle's *Anatomy* (12) it is regarded as the normal, though not constantly present. The Pectineus is described as consisting usually of two strata, which are separable externally, but joined internally, and united at the insertion. The origin of the deeper layer extends further inwards over the os pubis, hence the fibres of the two layers cross at an acute angle. This corresponds very closely to the arrangement found in the specimen I have described, the difference consisting only in the degree of separation. One does not find this double arrangement very often in the dissecting-room, though in many cases, especially in the lesser degrees of separation, it may be overlooked. Paterson (6) describes the muscle as occasionally consisting of two incompletely separated muscular strata. Winslow, in the copy of his Exposition (13) which I have seen, stated that he had seen the Pectineus double ("*Je l'ai aussi trouvé double*"), but the relative positions of the two divisions is not specified. In another edition or separate work (14) referred to by Testut and Macalister (15, *a*), it is stated that he had seen a bilaminar Pectineus.

The other condition of splitting has been described by Testut, who states that the Pectineus may sometimes be found in two

pieces on the same level, separated by an interval almost to its insertion. Macalister (15) has "seen it cleft into two parts," and mentions that this has been "also seen by Sömmering." In Quain's *Anatomy* (16) this variation is mentioned also, the Pectineus being divided into inner and outer parts.

Other variations consist in different degrees of admixture of the fibres of the Pectineus with fibres of other muscles, or of slips of fleshy fibres passing between the Pectineus and other muscles, principally those of the Adductor or Obturator nerve group. Winslow (14), in his description of the Pectineus, said that it mingled with fibres of the Adductor Longus at its origin, and with fibres of the Adductor Brevis at its insertion. Sir Wm. Turner (17) has described, in the case of a Negro, a muscular slip, three inches long, which arose from the inner border of the Pectineus, and joined the tendon of the Adductor Longus. Testut (11), later, described similar instances. He observed in two cases a fleshy bundle of fibres separate itself from the Pectineus shortly after its origin, and mix with the fibres of the Adductor Longus near the linea aspera. Macalister (15) has also seen a slip from the Pectineus passing over the Profunda femoris artery to join the Adductor Longus, and likewise fibres from the Adductor Longus to the Pectineus. He has also seen the Pectineus sending a slip to the Obturator Externus.

In the body prosected this session for the systematic course of lectures delivered by Sir William Turner, there was found a fleshy slip which separated itself from the inner border of the Pectineus near its origin, and blended with the Adductor Brevis on its anterior aspect near the upper border, close to its insertion.

Of connection with any other muscle, outside the Obturator group, I find only one instance, which is mentioned by Macalister (15, a), who has seen a slip from the Iliacus joining the Pectineus.

There are slight variations in the extent and position of the insertion of the Pectineus, *e.g.* partial insertion into the front of the capsule of the hip-joint (Macalister, 15, a). This may have some bearing on the theory of Bland Sutton (18) that the ligamentum teres is an evolutionary regression of part of the Pectineus muscle.

Comparative Anatomy.—Among mammals different varieties of the Pectineus muscle are found, and in certain monkeys variations have been found in the same species. In Cercopithecus and in the Chimpanzee (*Troglodytes niger*) Testut has several times seen a double Pectineus, and he describes the arrangement in the Chimpanzee; the two portions lay side by side, and were separated by a linear interval, which narrowed as they approached the femur. The Femoral artery lay on the outer head, while the Femoral vein lay along the interstice. This is almost identical with the condition of the Pectineus in the human subject in the second form of variation.

In some other mammals this is described as the constant arrangement. In the Raccoon (*Nyctereutes procyonoides*) the Pectineus has two heads, a long inner and a shorter outer (Meckel, 19). In Echidna also the Pectineus has two heads lying on the same level, an inner and an outer. Both come from the pectineal line, and the inner also from the symphysis pubis, and they are inserted into the Femur as far down as the third trochanter (Alix, 20). In some other mammals the muscle is single at its origin, and divided into two parts towards the insertion, unlike the arrangement of the split Pectineus in Man, where the tendency is towards division at the origin and union towards the insertion. In the Ox (*Bos taurus*) the muscle is single at the origin, but divides into two parts towards the insertion, the upper division being inserted into the upper part of the posterior surface of the shaft of the Femur, the lower extending as far down as the condyle (Chauveau, 21, *a*). In the Pig (*Sus domesticus*) the muscle is similar to that of the Ox. In the Koalo (*Phascolarctos cinereus*) and Opossum (*Didelphys virginiana*) the muscle is similar to that of the Ox, but the insertion is less extensive. It arises by a single rounded head, but divides after its origin, and is inserted as far down as the middle of the shaft of the Femur (Young, 22). In the Elephant (*Elephas indicus*) the mixture with fibres of another muscle is seen. The Pectineus takes origin between the Ilio-pectineal eminence and symphysis pubis, some of its fibres being closely connected with those of the Adductor Longus (Miall and Greenwood, 23). In the Horse (*Equus caballus*) the arrange-

ment at first sight may perhaps suggest bilaminarity. It is described by Chauveau (21, *b*) as bifid at its origin, with the Pubio-femoral ligament passing between the two parts. But the degree of bifidness only consists in that the Pubio-femoral ligament, passing through it near its origin, must have certain muscle fibres on the one side and certain on the other, while certain muscle fibres arise from the ligament. Ellenberger and Baum (24) do not describe it as even bifid; and Bland Sutton regards the Pubio-femoral ligament as part of the Pectineus itself which has undergone regression.

Nerve-supply. — Although the Pectineus under description got no branch from the Accessory Obturator nerve which was present, yet it got an Obturator supply by a branch which was given off from the inner side of the anterior division of the Obturator nerve, immediately after it had separated from the posterior division, and before it was joined by the communicating branch from the Accessory Obturator. The muscle also got the normal nerve-supply from the Anterior Crural. The branch from the Obturator passed downwards, outwards and forwards behind the nerve to the Adductor Longus, and in front of the nerve to the Adductor Brevis, and entered the deep surface of the posterior lamina about its middle. The branch from the Anterior Crural nerve was given off immediately below Poupart's ligament, followed the usual course, and entered the anterior lamina on its superficial aspect. In accordance with the relative size of the two laminæ, the branch from the Obturator was the smaller from the beginning; and it further reduced itself in size by giving off two very minute filaments to the Adductor Brevis before entering the Pectineus. No filaments of either nerve could be traced across from one muscular lamina to the other.

Relation to Nerve in Man.—The Pectineus, as a single muscle, is commonly supplied from the superficial division of the Anterior Crural nerve by one or two branches. One of the two branches may be given off in the abdomen and join the Accessory Obturator nerve (Gray, 7, *b*). It is also in some cases supplied from the Obturator nerve. Winslow (4, *c*) described a branch from the Obturator as of usual occurrence, but in his Exposition nerves are sometimes given a wide dis-

tribution, *e.g.* the Anterior Crural nerve, to which was referred
the supply not only of the Extensor muscles, but the Adductors
and the Semitendinosus as well (4, *d*).   In modern text-books a
branch from the Obturator nerve is described as of occasional
or of rare occurrence (Gray, 7, *a*; Macalister, 3, *b*; Cunningham,
25).   The supplementary nerve-supply may come from the
Accessory Obturator nerve when that is present (Ellis, 20),
but this is not always the case.   Schmidt (1, *a*) described a
branch from the Accessory Obturator when that nerve was
large.   In Cunningham's Manual it is said to be very rare to
find a branch from the Accessory Obturator nerve to the
Pectineus.   But in some cases the Accessory Obturator nerve
may supply nothing but the Pectineus, and the branch from the
Accessory Obturator to the Pectineus may be the exclusive
nerve-supply of the Pectineus (Paterson, 6, 9).   When the
Pectineus is a double muscle, a separate nerve is given to each
part.   The inner or deeper part is supplied from the Obturator,
the outer or superficial part is supplied from the Anterior
Crural nerve (Quain, 16 ; Paterson, 6).   I do not find described
a branch coming from the Obturator nerve to the Pectineus
when the Accessory Obturator nerve is present.

Relation to Nerve in other Mammals.—In mammals, so far as
I have read descriptions of the relation of the Pectineus to
nerve-supply, the Pectineus is supplied from either the Anterior
Crural or from the Obturator, but in several cases I have not
been able to obtain access to an account of the nerve-supply to
the muscle, either normal or abnormal.   In the monkey, how-
ever, the nerve-supply, as in Man, is from the Anterior Crural
nerve.   In the Gorilla (*Troglodytes Gorilla*), Orang (*Simia
Satyrus*), Gibbon (*Hylobates lar*), and Chimpanzee (*Troglodytes
niger*), Hepburn (26) could find no branch from the Obturator
to the Pectineus.   In *Macacus rhesus*, a large number of which
was examined by Sherrington (27), no Obturator supply to the
Pectineus was found.   In the Rabbit (*Lepus cuniculus*), the
nerve to the Pectineus is from the Crural nerve (Krause, 28).
In the Dog (*Canis familiaris*) the nerve-supply is from the
Obturator nerve (Ellenberger and Baum, 29).   In the Ox and
Pig, where the Pectineus is divided towards its insertion, the
nerve-supply is wholly from the Obturator (Chauveau, 21).   In

the Horse also the nerve-supply is exclusively from the Obturator nerve (Chauveau, 21 ; Ellenberger and Baum, 24).

CONCLUSIONS.

Taking into consideration the occasional occurrence of the Pectineus divided into two more or less distinct parts, each carrying with it a nerve-supply from different nerve-trunks, and that the Pectineus sometimes occurs as a single muscle with a double nerve-supply, if one may take nerve-supply as a guide, one is led to accept the view of Paterson that the two parts belong morphologically to the two different muscle-groups supplied by these two nerve-trunks, and that the single muscle, when it gets a double nerve-supply, does so in virtue of its compound character. This view is upheld by the occasional mixing of the fibres of the Pectineus with those of muscles of these groups, especially with those of the Obturator nerve group, either at the attachments of the muscles or by fleshy slips passing from one muscle to another. (It is unfortunate that in those cases where a fleshy slip passed either to or from the Pectineus, connecting it with other muscles, the nerve-supply could not be found and noted, as well as in the cases where the Pectineus is divided into two parts.) Further, at some remote antecedent time, the Pectineus may have normally consisted of these two parts completely fused, while each part retained its original nerve-supply as is now the case in the Brachialis Anticus of Man : and instances of the reappearance of that condition might be regarded as historical reversions. Moreover, since the Pectineus in certain mammals is normally supplied, exclusively, by one or other nerve only, one is led to think that the part belonging to one muscle-group may be developed to the exclusion of the other part, which is either lost, or may have rejoined the original muscle-group, or, following up the suggestion of Bland Sutton, may have undergone regression into a ligamentous structure, e.g. the pubio-femoral ligament in the Horse, the ligamentum teres in Man. A difficulty, perhaps not serious, presents itself here; that in one set of mammals one part has undergone regression, and in another set the other part; while one would expect, à priori at

any rate, that there would be more constancy in the selection of
the part which should remain muscular. It is possible that in
some mammals there exists, as a normal condition, a Pectineus
divided into two components, or fused into one with a double
nerve-supply; though, in those of which I have read descriptions,
a single nerve-supply is the rule, indicating the complete exclu-
sion of one of the two divisions of the muscle. In the Ox and
the Pig the Obturator nerve portion only is present. The division
into two parts is towards the insertion, and the muscle is not
in the same class of case as the occasionally divided Pectineus
of Man. From the point of view here considered, it may be re-
garded as accidental, possibly resulting from the greater extent
of attachment to the shaft of the femur; or it may be that a
part of it represents the Adductor Longus of Man. In the Dog
and the Horse the Pectineus belongs to the Obturator nerve-
group also. Ellenberger and Baum indicate that this muscle
may, in part at any rate, be the representative of the Adductor
Longus of Man. Chauveau regards the portion which lies in
the plane superficial to the pubio-femoral ligament as the homo-
logue of the Pectineus in Man. If this is so, it would correspond
to the portion of the Pectineus of Man which is commonly
absent, i.e. the Obturator nerve portion. In the Rabbit, in
Monkeys, and in Man the part belonging to the Anterior Crural
nerve-group of muscles predominates, generally to the complete
exclusion of the other part. In Man the normal Pectineus is
morphologically a segmentation from the Iliacus (Macalister, 3, e),
and is probably so in the Rabbit and Monkey. But in Man, as
a greater number of human subjects, through course of time, has
been dissected and examined than of any other species of
mammal, transition stages of the exclusion of part of the double
muscle have been seen and noted. As the Anterior Crural
nerve portion is the constant portion in Man, one may expect to
see, as is the case, the transitions taking place not in it, but in
the Obturator nerve portion:—Firstly, there is the original
fused condition of the two different portions seen in the small
percentage of cases where the Pectineus muscle, while consisting
apparently of one single undivided stratum, gets branches of
supply from both the Anterior Crural and the Obturator nerves
Next in order comes the condition in which there is a deeper or

internal inconstant portion, showing greater or lesser degrees of separation from the other portion, and supplied by the Obturator nerve. Thirdly, there is the union between the Pectineus and the Adductors Longus and Brevis and Obturator Externus, effected by slips of fleshy fibres passing from one muscle to the other, representing an imperfected attempt of a portion of one muscle to join wholly with the other. The process is nearly complete in those cases where there is merely the mixture of fibres of the Pectineus with those of the Adductor Longus at the origin, and with the Adductor Brevis at the insertion. Finally, there is the condition which is usually found; the Pectineus is separate and single, and has but the one nerve-supply.

The opposite assumption is tenable likewise: that the muscle is on the evolutionary road to become a compound muscle, and the series of steps, as seen in the variations, could be traced in the opposite direction, from the simple to the compound. The slips between the Pectineus and the Adductors would bear the same significance as portions of the Brachialis anticus joining the Supinator longus in the upper limb, such as have been described by Macalister (15, *b*), and of which I have seen two examples in different bodies during the last Winter Session. In support of this assumption there was the presence of a bilaminar condition of the Pectineus in a fœtus, constituting one of the stages of the development towards a fused compound Pectineus. This might have gone on *pari passu* with the development of the fœtus until at birth at full time, or in the adult state, the condition of complete fusion with a double nerve-supply would have been present. Considering the close association of the two laminæ and the age of the fœtus, it is more likely that it represents a stage in the inclusion of an Adductor portion into the Pectineus, rather than a stage in the separation of the Adductor element of the Pectineus, which might, at a later date, fuse with the Adductors proper. Less attention has been directed to the muscular than to any other system in the fœtus; otherwise, in muscles like the Pectineus, abnormal conditions, representing transitory phases in development, might more frequently be met with. The compound Pectineus differs, however, from the compound Brachialis anticus in being only occasionally present, and therefore anomalous; and anomalies are

rather to be classed as historical retrogressions than as evolutionary progressions.

The case described by Macalister, where the Iliacus gave a muscular slip to the Pectineus, is obviously one of an incomplete segmentation of the Pectineus from the Iliacus; and a comparable condition would be a slip passing from, say, the Adductor longus to the inner or deeper division of a divided Pectineus, or to an undivided Pectineus with a double nerve-supply.

The presence of an Accessory Obturator nerve, supplying part or whole of the Pectinous, offers no impediment to the view that the Pectineus may be a compounded muscle. In the cases where it takes on the whole supply, it is given off from the roots of the Anterior Crural nerve, as Paterson has pointed out; and it practically amounts to an intra-abdominal origin of the nerve to the Pectineus from the Anterior Crural, similar to that described in Gray's *Anatomy* as joining the Accessory Obturator, and that described by Macalister, given off within the abdomen with the Internal Cutaneous nerve. In those cases where the Accessory Obturator comes from the roots of the Obturator nerve and supplies the Pectineus, it would merely signify an intra-abdominal origin for the Obturator branch to the Pectineus, similar to that of the Anterior Crural, and the Pectineus, in such a case, is a muscle made up of two parts.

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COMPLETE ABSENCE OF THE SUPERFICIAL FLEXORS OF THE THUMB AND CONCURRENT MUSCULAR ANOMALIES. By H. S. HALL, B.A., *Pembroke College, Cambridge*. (PLATE XXXII.)

A RECENT dissection of an upper limb in the Cambridge University Anatomy School exhibited a very anomalous condition of the musculature of the thumb.

The subject was a well-developed male; and when the time came for removing the skin from the hand, it was noticed that the thenar eminence was unusually lacking in prominence. A small amount of dissection revealed the fact that this was due to the complete absence of the superficial flexors of the thumb, viz., abductor pollicis, opponens pollicis, and the superficial head of flexor brevis pollicis. Consequently, on removing the skin, the entire length of the metacarpal bone of the thumb was displayed. Moreover, the short stout branch of the median nerve, which in normal cases supplies these muscles, was in this subject completely absent.

This condition has, I think, only once been recorded.[1]

The condition was unaccompanied by any hypertrophy of the neighbouring muscles. The remaining thumb muscles were in appearance quite normal. However, at a later stage in the dissection, some additional peculiarities of musculature were displayed.

The tendon of extensor ossis metacarpi pollicis was double, as is not infrequently the case. From the external tendon a small quadrilateral muscle some 15 mm. square passed transversely inwards, and was implanted on to the superficial aspect of the anterior annular ligament. The accompanying photograph shows this muscle clearly. I have been unable to find any recorded instance of a muscle exactly similar to this.

In view, however, of the frequency with which muscular slips from the superficial group of thumb flexors (especially abductor pollicis) are found with attachments to the tendon of extensor

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[1] Fromont, "Anomalies musculaires multiples de la main," *Bull. de la Soc. Anat. de Paris*, Avril–Mai, 1895, t. ix. fasc. x. p. 395..

ossis metacarpi pollicis, it is possible that this anomalous slip
was an aberrant representative of one or all of the missing
flexors. Unfortunately, the nerve supply to this anomalous
muscular slip could not be found. It is interesting to note that
this slip, together with the extensor ossis metacarpi pollicis, to a
certain extent provided a functional compensation of the missing
group. The resultant of the pulls of the two muscles is in-
dicated in the accompanying diagram. Thus the extensor ossis
metacarpi pollicis pulling, roughly speaking, in the line of the
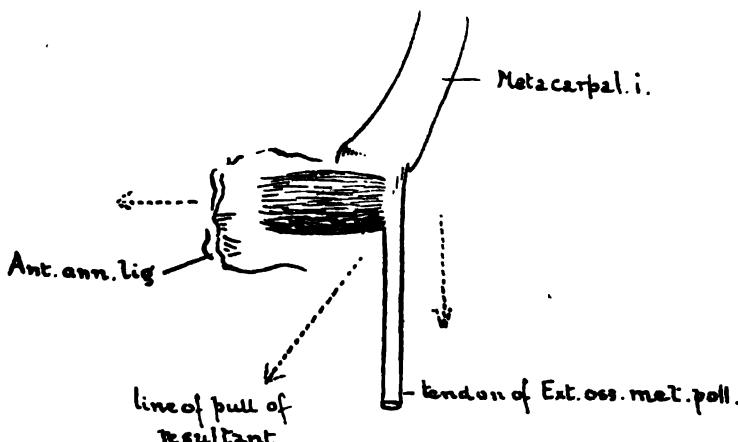
forearm, and the anomalous muscle at right angles to this, the
resultant of these two would be equivalent to a muscle pulling
diagonally across the wrist in the direction of the arrow, as
shown in the diagram.

Further dissection exposed an additional slip of muscle fibres,
apparently arising from the fascial sheath of the tendon of
flexor longus pollicis, and distally connected with the tendon of
insertion of the indical lumbrical muscle.

A somewhat similar accessory muscle to the indical lumbrical
connected with the metacarpo-phalangeal ligament of the thumb,
and occupying the web between the index finger and thumb,
has been described by Arbuthnot Lane,[1] and a slip from the
flexor longus pollicis to the first lumbrical muscle has been
noted by Wood and Macalister. But in neither of these cases

[1] *Jour. of Anat. and Phys.*, vol. xxi. p. 674.

[PLATE **XXXII.**

Mʀ H. S. Hall.

were any concurrent anomalies in the musculature of the hand noted.

From this we may either conclude that in our subject the presence of the additional lumbrical slip was a mere coincidence, and had nothing to do with the other peculiarities mentioned, or else we may regard this extra lumbrical slip as being a displaced slip of the superficial flexors of the thumb.

This is a point, I think, which cannot be definitely settled, but in any case the presence of the extra lumbrical slip is interesting.

In conclusion, it may be mentioned that the hand showed no signs of having received any injury to account for these anomalies. The superficial palmar arch was, however, completely absent.

The left hand of the same subject exhibited no abnormal arrangement of the muscles.

A METHOD OF OBTAINING UNIPLANAR SECTIONS WITH THE ORDINARY ROCKING MICROTOME.

By W. Sampson Handley, M.S. Lond., *Surgeon to Out-Patients at the Samaritan Free Hospital for Women and Children.*

The greatest disadvantage of the ordinary Cambridge Rocking Microtome has always been that its sections, instead of being uniplanar, are segments of a cylinder.

If the piece of tissue to be cut is a large thin slice, having an area, for instance, of a square inch, and embedded on the flat, its peripheral part may be entirely sliced away before the knife begins to cut the central portion of the tissue, and it may thus be quite impossible to obtain a section of the whole area of the piece embedded.

Where the piece of tissue is thick enough to be ' turned' by the knife to a smooth convexity before its edges are entirely shaved through, a complete section of the whole area of the piece is obtainable. But the section is so far from being uniplanar if the piece is a large one that a serious distortion is introduced which may obscure the relations and introduce fallacies in the interpretation of the microscopic appearances.

These disadvantages have been remedied in the recently introduced rocking microtome, in which the axis of rotation of the rocking arm is at right angles to the edge of the razor, instead of lying parallel to it as in the ordinary ' Cambridge Rocker.'

Since, however, for many workers the latter may be the only microtome available, it seems worth while to describe a way of obtaining with this type of microtome uniplanar sections of large area. I have not seen the method described, though doubtless such a simple device may have occurred to many.

It essentially consists in embedding the slice of tissue to be cut on a cylindrical surface, corresponding to the curve described by the rocking arm of the microtome.

A squared block of paraffin, sufficiently large to contain the

piece of tissue to be cut, is fixed on the rocking arm, with its centre truly in the axis of the arm, with its upper edge horizontal, and with its free surface forming a plane at right angles to the axis of the arm. These points can be judged with sufficient accuracy by the eye.

This pattern-block is now cut in the ordinary way until its cut surface has acquired the convex cylindrical form, and complete sections of it are being cut by the razor. It is now dismounted, covered with thin tinfoil, and surrounded by a projecting rim of stamp-paper. A mould with a convex cylindrical floor is thus produced, and into this plaster of Paris is poured as it stands on a level surface.

When the plaster has set, it forms a square or oblong block with one concave cylindrical surface. Tinfoil is swagged down upon this surface, and the edges of the block surrounded by a rim of stamp-paper. The embedding mould is now ready.

The slice of tissue used is very thin, say not more than ⅛-inch thick, for two reasons. First, since the sections are uniplanar, *very much thinner pieces may be used*, which is one great advantage of this method. Secondly, unless the piece of tissue is thin, it does not adapt itself properly to the concave floor of the embedding mould.

During the process of embedding it is necessary to hold down the slice of tissue with hot needles until the paraffin has set sufficiently to hold it in its curved position on the floor of the mould. While the paraffin is cooling, the mould must of course stand on a horizontal surface.

The paraffin block thus obtained must be detached from the mould and fixed truly on the rocking-arm, in a position exactly corresponding to that of the pattern-block from which the mould was made. The razor will at once commence to cut complete sections of the curved surface of the block.

The method is much simpler than it sounds in description, and when once the plaster mould is made, takes no more time than [embedding on a flat surface. In this way I have obtained uniplanar sections from blocks 1¼-inch in diameter without difficulty.

I cannot conclude without expressing my belief that the

habitual use of sections of large area, in which the naked-eye relations of the parts could be easily traced, would be of great advantage in pathology. With the small sections at present generally used, the view of the pathological condition obtained may be compared to that of the interior of the bladder given by a single endoscopic field. The same thing is probably true in normal histology.

ARCHÆOLOGIA ANATOMICA.

IX.

HILUM.

HILUM is a good and ancient classical word. It is given by Pompeius Festus (*de Significatione verborum*, ed. Gothofried, p. 296), with the definition *putant esse quod grano fabae adhaeret, ex quo nihil et nihilum*. As this work is for the most part an abbreviation of the oldest Latin vocabulary, that of Verrius Flaccus, who lived in the Golden Age, about the beginning of the Christian era, this gives the word a respectable antiquity. From the insignificance of the bean seed-stalk it came to signify metaphorically anything very small, so that a fourth century lexicographer, Nonius Marcellus, defines it in his work, *de Compendiosa Doctrina*, ii. 121, as "*breve quoddam.*" It had got this sense in the oldest Latin writers; thus Ennius writes in his *Annales*:

> *terraque corpus*
> *quae dedit ipsa capit, neque dispendi facit hilum.*

In like manner Lucilius the satirist, writing more than a century B.C., says, *quod tua laudes culpes non proficis hilum* (xxx. 33); and in xiv., *hilo non rectius vivas.*

The author who uses the word most frequently is Lucretius. He employs it in the sense of a minute particle or amount, like our old English word *whit*. Speaking (iii. 220) of the soul as consisting of very small seeds, so inwoven in the body that its withdrawal does not alter the corporeal weight, he says:

> *incolumem praestat nec defit ponderis hilum.*

Again, when speaking of changes of mind, he predicates that they necessarily require the addition of a new part, the re-arrangement of components or the subtraction of a *hilum* (iii. 514), but the Immortal wills not such a withdrawal,

> *nec tribui vult*
> *immortale quod est quicquam neque defluere hilum.*

In iv. 515 he describes the mischief done to a building by the use of an incorrect measuring rod, *si ex parti claudicat hilum.* So also, iv. 379, *nec tamen hic oculos falli concedimus hilum,* "nevertheless we do not admit the eyes to be deceived a jot." In iii. 783 and v. 1408, *neque inter se contendant viribus hilum,* and *neque hilo,* the word is construed with the negative particle, as it is by the unknown poet quoted by Cicero (*Tusc. Disp.,* i. v. 10),

> *Sisyphu' versat*
> *saxum sudans nitento neque proficit hilum.*

Another ancient Latin author who employs the word in various senses is Varro, who gives it as the name of a small kind of sausage (v. 111). *In quo quod tenuissimum intestinum fartum hila ab hilo dicta.* Later on he describes another kind, probably made in the same narrow part of the gut, which he calls *longavam quod longius quam duo hila.* As if to emphasise that this sausage is so called from its size, he quotes the passage from Ennius above given. Farther on (113) he uses the word in the sense of something small when speaking of filum, *Filum quod minimum est hilum; id enim minimum est in vestimento.* This sense he also expresses in speaking of its negative derivatives, *nihil* and *nihilum* (ix. 54 and x. 81). In Stephanus' *Thesaurus, s.v.* Hilum, the author says, *Varro tamen de L.L. 4, Hilum significare censuit Medullam ejus ferulae quae Asphodelus vocatur,* but I cannot find the passage referred to.

Charisius, in his *Ars Grammatica* (ed. Putsch, i. p. 79), supposes that Varro confounded *hilum* with another word *hilla,* but it is plain that he specially quotes Ennius to show the sense in which the word was used. *Hilla,* according to Pliny, xi. 79, is the intestine, a word not given by the oldest lexicographers, but which was used in the sense of sausage in the familiar lines of Horace (*Satire* ii. 4. 60):

> *Perna magis et magis hillis*
> *flagitat immorsus refici.*

The commentator Acron remarks that the hillæ are *salsa intestina hirci* (ed. Havthal, ii. 288). Macrobius (*Somn. Scipion.* vi. 77) says that hilla is a diminutive from *hira,* the large intestine; see Plautus (*Curculio,* ii. 1. 23).

Plautus also uses *hillae* in the sense of sausages when he

speaks of *hillas infumatas et sumen.* See also the line from the
Catularius of Decius Laberius :

> *adolescente nostro caedis hillas.*

And another from an unnamed poem by the same author :

> *lambum item*
> *hillam cocum si lumbum adusset.*

In Ausonius Popma's *de Differentiis verborum,* s.v. *nihil,* he says,
est autem hilum proprie medius volae scrobiculus.

The foregoing study of the word is enough to show that
hilum is a good classical Latin word, and throughout the whole
range of ancient and mediæval literature there is no such word
as hilus.

As an English word, hilum was used in the sense of a small
amount in Daniel Pell's curious work, "Πελατος; or, an Im-
provement of the Sea," upon the nine nautical psalms, published
in 1659. He speaks of " unhewn sailors, that have no more
than a hilum of goodness in them."

The first use of the word as a scientific term known to me is
in Linnæus' *Philosophia Botanica,* 1751, p. 71. Here it is used
as the name for the spot of attachment of the seed, somewhat
in the original sense given by Festus. I cannot find any earlier
use of the name; it was apparently not in use in Bradley's time
(1728), and Gaertner (i. cxiii) attributes it to Linnæus, and
prefers it to the Malpighian term *fenestra.* In this sense the
word is familiar to botanists, who almost always use the Linnæan
form hilum (but I note that in German de St Pierre, 1870, the
alternatives *hilum, hilus, hylum, hylus* are all given).

It is easy to trace the stages by which the word became
applied to the area of attachment of the kidney. Eustachius
(*Opusc. Anat.,* Venet., 1564, p. 31) compares this organ as to its
shape with the *Faseolos* or kidney-bean ; and when describing its
margins he says, *interius vero, qua vena et arteria in eos inseritur,
simi à natura facti sunt et in eam retusae lineae speciem curvati,
quae treicijs arcubus non inepti comparari potest.* Galen had,
before this, called the hilum of the kidney τὰ σιμά; other authors
called it in later times *concavité* (Winslow), *sinuosité* (Portal),
porta renis (Fallopius), etc.

The Eustachian description is adopted and somewhat para-
phrased by Haller (1765, xxvi. § 1. 4), who says, *Homini renis*

figura est, quae phaseoli, ut nempe facies anterior et posterior compressa sit, et utroque hinc per aciem convexam semielipticam uniatur, inde per hilum quo interior longitudo renis exsculpitur.

Here he is, as far as I know, the first to apply the Linnæan name to this bean spot on the bean-like kidney. In the sentence just quoted the word is accusative, but in continuing the Eustachian description he makes its nominative hilus, *Hilus recte cum arcus Turcici.* Later describers have used the same comparison : thus Cruveilhier has " La figure du rein ne saurait être mieux comparée qu'à celle d'un haricot dont le hile serait en dedans."

That the use of the Linnæan name was suggested by the bean simile is confirmed by the fact of this word being used by Haller of the kidney only, not of the spleen or liver. The transverse fissure of the latter is with him the portæ. He uses Galen's plural, that author having described the portæ as two (*de Formatione Fœtu,* iii), and Haller speaks accordingly of the vena portarum.

Once started, the error was propagated by Meckel, and it is to be found also in the works of Lauth, Krause, Henle, and Sömmerring. Hyrtl, in his *Onomatographia,* recognises that *hilum* is the proper word, but he has not the courage of his conviction, and uses *hilus* in his *Topographical Anatomy.* The French authors, as they appropriate and gallicise the word *hile,* are saved from the necessity of choice between the two. English writers for the most part use the Linnæan *hilum.* It is so in Knox, Wilson, Heath, Morris, Gray, and in Todd's Cyclopædia, as well as in Ellis (*pace* Murray's Dictionary, *s.v.*). Quain is impartial, using *hilus* in the 1882 edition, and *hilum* in that of 1896. Cleland also follows the Germans.

Reviewing the history of the word, there cannot be the shadow of a doubt that Linnæus was correct in the form, if not in the usage, of the word, and that the mistake in gender was a slip of Haller's ; *quandoque bonus dormitat Homerus.* Had he meant to make a new word he would have said so, and explained his intentional departure from the acknowledged form. Whether, as the *hilum* of the kidney is not exactly the same as the *hilum* of the bean, there is need for a new word is a debateable point ; but until this is definitely agreed to, and *hilus* put on the same

footing etymologically as Paracelsus' word *gas*, frankly, as a barbarism, those who are interested in the maintenance of some degree of classical purity in the nomenclature will do well to adhere to the form of the word that is sanctioned by the usage of twenty-three centuries.

This is not the place to discuss its etymology; but in view of the relations of *h* and *f* in early Latin words, it may be that Festus has hit on a correct parallelism, and that it is a variant of the word, which has otherwise become perpetuated in its Sabine form. Compare *hircus* and *fircus*, *hædus* and *fædus*, *hordeum* and *fordeum*, etc.

A. M.

THIRTEENTH REPORT ON RECENT TERATOLOGICAL LITERATURE. By BERTRAM C. A. WINDLE, M.D., Sc.D., F.R.S., *Professor of Anatomy in the University of Birmingham.*

I. GENERAL.

IN an address by SCHATZ (i.), of which a summary has appeared in the *British Medical Journal*, the question has once more been raised as to how far *Mythology is indebted to Teratology* for some of its figures. This matter has previously been dealt with by Berger de Xivrey in his *Traditions Tératologiques*, by Bland Sutton and by Ballantyne. Schatz identifies the siren with the sympodial fœtus, the centaur with the fœtus with four lower extremities, the gorgon head with an acormic placental parasite, Janus with the janiceps fœtus, and so on. The speculation is one of considerable interest. RABAUD (ii.), in a lengthy paper dealing with *experimental determinism and the individuality of the germ*, says that, judging by many of the results obtained by experimenters, one would be tempted to believe that the fundamental principle on which all experimental science depends is not applicable to teratogeny. In fact, it would seem as if the artificial production of abnormal embryos was subject to no law, the same teratological types being produced by the most varied causes. After stating this difficulty, the writer proceeds to examine the classes of experiments which have been entered upon, and particularly those which have been carried out upon hens' eggs, which —as he very aptly points out—are not really ova but multicellular organisms at the time when experiments are made upon them, a fact which must always be borne in mind when estimating the evidence derived from this quarter. He concludes that the artificial production of monstrosities is bound up with a strict and precise determinism which experimenters must master, though as yet they have not done so. The greatest difficulty, he adds, will not be to lay down the rules of determinism, so much as to connect the experimental facts with the spontaneous, and above all with those met with amongst the mammalia, and particularly in man. RABAUD (iii.), in another paper, deals with the *relationship between the pathological and teratological states*, and points out that in considering the production of congenital conditions, one must not merely take into account the factor concerned in producing the disturbance. The embryonic organism does not necessarily react in the same way as the adult organism, and its reactions depend as much on the intensity of an agent as upon its specific character. There are two categories of congenital states strongly opposed to one another, and carefully to be

distinguished.   These two states may be the result of the same or different agents, capable or not capable of producing in the adult a pathological alteration.   They are on the one hand abnormalities, and on the other maladies.   There is also a third category, in which abnormality and malady are mixed up with one another.   THOMSON (iv.) points out, in a paper on *Defective Co-ordination in Utero*, that there are at least three types of congenital malformation of hollow viscera, in which the main anatomical abnormality present consists in very great muscular hypertrophy, for which no permanent organic cause is discoverable.   These are, (*a*) Congenital hypertrophy of the bladder, with dilatation of the ureters and renal pelves, and with no organic obstruction.   (*b*) Congenital hypertrophy of the colon, with no organic stricture.   (*c*) Congenital hypertrophy of the pylorus and stomach wall.   The writer seeks to explain these conditions by attributing them to a functional cause, viz., a disturbance of the normal co-ordination.   RABAUD (v.) has made a long and critical study of the question of the *teratological nature of malignant tumours.* Without denying the possibility that an arrest of development may become the origin of a tumour, he thinks that such a phenomenon is probably rare, since its occurrence is surrounded by so many difficulties.   In any case, for such a group of elements to develop into a malignant tumour, the intervention of an external agency is necessary. But if this agent can produce the same effect upon any group of adult cells, it is difficult to. see why the theory of retained embryonic elements is required.   But in some cases it does seem as if, by a simple process of excessive growth, an embryonic inclusion may develop into a tumour, in this case a truly congenital tumour. SELIGMANN (vi.) has contributed a paper dealing with *Albinism* amongst Melanesians and Polynesians, in which he shows that in this part of the world as elsewhere the condition is hereditary.   Partial albinism occurs, but more rarely than the complete form.   The subject of *Fœtal Bone Disease* was dealt with at the annual meeting of the British Medical Association during the last year in a discussion opened by BALLANTYNE (vii.), for an account of which the inquirer must be referred to the Journal of the Association.   REGNAULT (viii.) gives a few notes on *achondroplasia*, in connection with the cases of two subjects with asymmetry of the pelvis.   The antero-posterior measurement was diminished.   In the lower extremity the legs were relatively shorter than the thighs.   BLANCARD (ix.) discusses *the rôle of the amnion in the production of abnormalities*, a part which he believes that it undoubtedly plays.   It may act by compression, by the formation of adhesions, or by the production of constricting bands. Compression leads chiefly to deformities, irregularities, and displacements of external parts.   Adhesions are preceded by rubbing; inflammation follows, and the production of cicatricial tissue.   Traction may also be exerted, and deformity added to destruction.   The part played by bands is that of strangling and sectionising portions of the body.   BAUMGART (x.) describes a case of *vesicular mole* accompanied by ovarian cysts, and states that he believes there is a connection of cause and effect between the two, though at present no scientific

explanation of the relationship is forthcoming. GALLANT (xi.) describes a most remarkable case of *half-embryo*, which he states to be unique (the present reporter believes that he is right in this). The whole right side of the trunk was absent, and the remainder was so curved that the left lower extremity occupied the position of the right upper with respect to the head. Perhaps this will be better understood if it is stated that the figure appears to represent a fœtus with the entire of the body below the pectoral region removed. The single foot was provided with seven toes. The head was anencephalic. It is unfortunate that no account is given of any dissection of this very remarkable specimen. COOKE (xii.) adds another to the cases of *complete transposition of the viscera*. RABAUD (xiii.) contributes a very lengthy and important monograph on the subject of *cyclocephaly*. The embryology of the condition is fully worked out, and the paper is illustrated by numerous figures. This is a most valuable contribution to the subject, but unfortunately not of a kind which can be easily abstracted. But it must be read by every person working at this particular corner of teratology. TARUFFI (xiv.), in three large monographs, has dealt with the subject of *Hermaphroditism*, on the lines made familiar by his monumental *Storia della Teratologia*. The classification which he adopts is as follows :—

ANATOMICAL HERMAPHRODITISM—

    I. Specific Hermaphroditism of the sex-glands. (True Hermaphroditism.)
        A. True Bilateral. A testis and ovary on each side.
        B. True Unilateral. On one side a testis or an ovary, and on the other both.
        C. True Lateral (Alternate). A testis on one side and an ovary on the other.
    II. Aplastic Hermaphroditism of the sex-glands. (Atrophic or Neuter Hermaphroditism.)
    III. Pseudo-Hermaphroditism.
        A. Male.
            (*a*) Persistent Mullerian duct.
            (*b*) Feminine external appearance.
        B. Female.
            Persistent Wolffian duct.

CLINICAL HERMAPHRODITISM—

    I. External Pseudo-Hermaphroditism.
        A. In man : Ectopia vesicæ.
            Perineo-Scrotal Hypospadias.
            Gynæcomastia.
             Feminism.
        B. In female.
    II. Heterotopic Pseudo-Hermaphroditism (Taruffi).
    III. Psychic Hermaphroditism (Krafft-Ebbing).
    IV. Sexus Incertus.

KRABBEL (xv.) records the case of a supposed male, a teacher in a school, short, but with a moustache and beard. There was a distinct penis, with extreme hypospadias, no scrotum nor testicles. There were well-formed labia, and under chloroform a small vagina and cervix were detected. An operation having been performed for an abdominal tumour, this proved to be a cystic ovary. There was a small uterus, broad ligament, etc. Another case of *Hermaphroditism*, in which the diagnosis of sex was made post-mortem, is recorded by WESTERMAN (xvi.). The patient was aged 30. The penis was 2½ ins. long. The urethra opened into the perineum, whilst along the under surface of the penis ran a groove. From each side of the penis proceeded a cutaneous fold. The two surrounded the urethral meatus and a small opening behind it, and united to form a posterior commissure. The second opening was small, and led to a canal which ran in the posterior wall of the bladder; there was an indication of a hymen. The hair was thick on the pubes and anus, and covered the inner side of the rudimentary labia, which did not contain testes. A left Fallopian tube, 2¾ ins. long, ran outwards from the posterior wall of the bladder, with distinct fimbriæ, round ligament, and mesosalpinx. There was a slight thickening of the tissues at the site of the ovary. The thickened tissue contained no epithelium, follicles, or Pfluger's tubes. Only when the peritoneum was dissected off the back of the bladder was the uterus (under 2 ins. long) and the vagina (3 ins.) detected; the latter was pervious for an inch or so at the abdominal end. In the right inguinal canal lay an open processus vaginalis, which contained a bean-shaped organ. On further examination that organ was found to be invested with a tunica albuginea. It contained a quantity of well-formed tubules, and a trace of epididymis was detected in the mesosalpinx. The tubules contained no spermatozoa. The patient was clearly a male. ROGER (xvii.) adds a further case of *Hermaphroditism.* The subject was supposed to be a boy of 19. The external genitalia were like those of a male, save for the pubic hair, which conformed to the female type. There was a small vagina internally, with a normal uterus connected with it. On the right side was an ovary, on the left neither ovary nor testis. HAMAY (xviii.) records a case of *gynæcomastia* occurring in a negro. WILLIAMS (xix.) has compiled a valuable list of cases of *precocious sexual development* in a paper dealing with this subject. In some instances menstruation commenced immediately after birth. HARRISON (xx.) has a paper, with illustrations, dealing with a *tailed* baby. The appendage was removed at the age of six months, and then measured 7 cm. It was only 4·4 cm. at birth, so was growing fairly rapidly. It was capable of contraction. A microscopic examination was made after its removal. The skin and its appendages were normal. Internally there were blood-vessels, nerves and striated muscular tissue (a few bundles). There was no trace of anything like a medullary cord or of notochordal tissue. DENIKER (xxi.) calls attention to the observation made by Balez in 1873 of the *pigmentary patches* of the sacrolumbar region of Japanese. The patches are blue or grey, and are said to be present in all Japanese babies. They appear about the

fifth month of intrauterine existence, and generally disappear between the second and the fourteenth year, but may persist all the life. Later, Hansen has called attention to similar patches on new-born Esquimaux children. Matignon has observed the same thing in China, and v. Bulow in Samoa. CUTORE (xxii.) has a very elaborate monograph on the skeleton of an *anencephalus*. KATZ (xxiii.) describes a *symelian fœtus*, also the subject of anencephalus. There were no kidneys, bladder, ureters or urethra. Testicles were present but no penis. The great intestine ended at the promontory of the sacrum. All bones of both lower extremities were present, a some-what unusual condition. SZAWLOWSKI (xxiv.) records the following rare *abnormalities in connection with the vertebral column* : (1) a rudimentary rib, articulating with the fourth cervical vertebra ; (2) a transverse foramen in the fifth lumbar and first sacral vertebræ; (3) a process from the ventral surface of a coccygeal vertebra. DWIGHT (xxv.) also records a case of a *transverse foramen* in a fifth lumbar vertebra. He is of opinion, however, that this was a twenty-fifth vertebra, whilst the last-named author's was a twenty-fourth.

II. DUPLICITY, ETC.

WALLA (xxvi.) records a case of *unioval triplets*, male, with common placenta and chorion and three separate amniotic cavities. A still more abundant output comes from Japan in the case described by SATO (xxvii.) where a woman aged 37, who had previously had eight labours, gave birth to five children at her ninth pregnancy. The first, third, and fifth of these were male, the rest female. A paternal cousin and her daughter had both been the mother of twins, but there was no other evidence of heredity in multiple bearing. LICHEM (xxviii.) records two cases of *fœtus papyraceus*. In the first there was a history of heredity in twinning, but not in the second. In the first the placentæ were separate, in the second there was a common placenta and the insertion of the cord of the imperfect fœtus was velamentous. A further *case of the same kind* is recorded by SONN-BERG (xxix.), remarkable for the small size of the *fœtus papyraceu*, which measured only about two-thirds of an inch. The case of the conjoined twins *Radica-Doodica* having already been mentioned in these reports, attention may now be called to the fact that they were separated from one another during the year by surgical means. An account of the operation, with notices of other similar cases, will be found in the *British Medical Journal* (xxx.), wherein are also notes on early instances of adult duplicities, the *Biddenden Maids* (xxxi.) and the *Twin Sisters of Fosscote* and *Scottish Brothers* (xxxii.). LESBRE and FORGEOT (xxxiii.) record an instance of the birth of an *acephalus* with a normal calf. It consisted of a malformed head, with obvious lower jaw and a portion of intestine. There were rudiments of brain and spinal cord. A case of *fœtus included in the Ascending Meso-Colon* is narrated by AHRENS (xxxiv.). The tumour taken from a girl of seventeen was as big as a man's head, and

held nearly seven pints of a thick brown fluid. Its walls contained all the component parts of the stomach, and its epithelium corresponding not merely to that of the viscus just named, but also to the mouth, œsophagus, bronchi and trachea ; so that the girl was provided with a second alimentary canal, or at least a large part thereof, quite unconnected with the normal passage. POPESCUL (xxxv.) describes a *terotoma* growing from the sacral region of a fœtus, which tumour was twice the size of a fœtal head, and much impeded the course of delivery. JOHNSON (xxxvi.) gives an interesting account of *axial bifurcation in snakes.* Thirteen two-headed snakes are described by means of skiagraphs, and the cases of others are mentioned. The abnormality seems to be more common in some species than in others, and the point of bifurcation is more likely to occur in the cephalic half of the snake, and between six and thirteen per cent. of the entire length from the cephalic end. The point of bifurcation of the vertebral column is a good deal more posterior than would be supposed from an external examination. The skulls frequently appear united externally when in reality they are not so. No specimen of posterior duplicity has been described, though three of antero-posterior are recorded. [*Note.*—In this respect the conditions resemble those found in fishes.] LESBRE (xxxvii.) publishes a series of observations on *pygomelia* as observed in two cows, a cock and a duck, the latter looking as if it actually walked on four legs. An attempt is made at the classification of different forms of the malformation, various names having been assigned according to the point of attachment of the appended limbs. The writer thinks that all may be reduced to the single condition of posterior duplicity, which he proposes to call pelvadelphy. ANTHONY and SALMON (xxxviii.) consider *pygomelia* to be a double monstrosity, symmetrical and lambdoidal, of the syncephalous variety. This view is based on the following proofs :—(*a*) The presence above the point of confusion of the axes of double abdominal organs, showing the double nature of the subject. (*b*) The peculiar orientation of the supplementary limbs, which do not pair with one another, but with the external limbs. (*c*) The presence between each external limb and the adjacent internal limb of a cloacal orifice. (*d*) The insensible transition which exists between the most reduced pygomele and a janiceps. There are, however, pygomeles of a parasitic origin, without double abdominal viscera. Consequently, the writers think that the term 'pygomelia' should be dropped, and that of 'pelvadelphus' substituted in the case of pygomeles of the syncephalous group. ALLAN (xxxix.) has described a human *pygomele* aged 14. He has a third leg attached to the back and sides of the pelvis, on which he can support himself. Anteriorly there is a normal penis with scrotum, and posteriorly a second penis with cleft scrotum, containing two well-developed testicles. There is one anal aperture. A metatarsal bone and three phalanges are connected by cartilage with the femur of the accessory limb. RABAUD (xl.) deals with a case of *sternopagous chick* and with the condition of monomphalism in general. The specimen was found in an egg of four days' incubation, though the individuals were

actually somewhat behind the development normal for that period. The heart condition is interesting, for that organ only receives two vessels inferiorly, one from the embryo of the right, the other from its fellow. These are obviously the two omphalo-mesaraic veins. The condition is not due to the fusion of four trunks. The fact is that there is only one circulatory system for the two united embryos, and this cannot be said to have arisen by the fusion of two stems. There is no trace of any such thing even in this very early embryo, in which there never has been anything but a single cardio-vascular apparatus for the two individuals. Turning to more general conclusions, the writer deals with the fusions which, as Lereboullet has shown, may take place in fishes. These fusions are not the cause of the duplicity, but, on the contrary, its consequence. The duplicity itself proceeds neither from a coalescence nor from a fusion. To put the matter briefly, the genesis of a double form is single; the two components form a whole from the commencement; it is one and the same organism, having its own methods of development. The two nervous axes are independent one of the other in these cases (sterno-pagi), but as they both exist on a common embryonic area, the embryos of which they represent the anlagen find themselves obliged to develop at the expense of regions common to both, so that they must have certain organs in common, wholly or partially, by necessity, and without any phenomenon of fusion. From this community of development result certain special processes. The double malformation constitutes a single organism in two parts, each closely connected with the other, developing in concert under conditions rendered inevitable by the duplicity. Pressure may afterwards cause secondary fusions, but these unions are the consequence, not the cause of the duplicity.

RABAUD (xli.) gives the details of an instance of *fission* in the embryo of a chick, confined to the spinal cord and muscle-plate. The posterior limbs were not affected by the duplicity, there being only two. SCHMITT (xlii.) has a paper on the *gastrulation of double trout embryos*, with special reference to the concrescence theory. He concludes:—(1) That the germinal areæ which give rise to double embryos are no larger and contain no more material than the normal. The invagination of the entoblast begins on them simultaneously in two places, and the lateral lip of one blastopore unites with that of the other in a symmetrical plane. (2) The embryonic anlagen grow slowly forward over the yolk, whilst the segments of the equatorial ring grow the more rapidly the further they are from the embryonic anlagen. (3) The material of the equatorial ring, from the commencement of embryonic development, passes into the embryo, which elongates backwards. There it is mainly utilised for the formation of mesoblast. (4) The very marked flattening of the cells of the vitelline membrane causes a displacement of the embryos in a direction from the originally animal to the originally vegetable pole of the egg. (5) The position of the first embryonic anlagen determines in all cases the later arrangement of the double formation. The nearer the anlagen were originally to one another, the sooner the embryos come in contact with one another. (6) Each embryo grows as a separate

entity, but the opposed sides, and especially the mesoblast between, have a less free development than the outer edges. (7) The concrescence theory cannot by itself explain any kind of double embryo. BROMANN (xliii.) has a most suggestive and admirably illustrated paper on *atypical spermatozoa*, which he divides into four groups :— A. Differing from the normal only in size—giant and dwarf spermatozoa. B. Possessing a single head but two or more tails. C. Possessing two or three heads, with either a single or a multiple tail. D. Single and of normal size, but presenting some abnormality of shape. In the latter portion of the paper the question of the relation of these abnormal spermatozoa to the origin of homologous twins is discussed.

III. HEAD AND NECK.

HAUSHALTER and BRIQUEL (xliv.) give an account of a case of meningo-encephalocele projecting as a hernial structure from the left frontal eminence of a new-born child. Besides the tumour there was very serious malformation of the face, all that portion of which between the lower jaw and lip (both of which were well-formed) and the forehead formed a single cavity with irregular margins. NORSA (xlv.) describes two cases of congenital *encephalocele* affecting white mice. The region affected was partly the vault and partly the occipital portion of the skull. A case of *porencephaly* is fully described by SHIRRES (xlvi.). The right hemisphere of the brain was well-convoluted and normal. On the left side the convolutions of the mesial and orbital aspects seemed to be intact, if poorly developed. The whole region of the fissure of Sylvius was occupied by a cavity, the remains of a cyst which did not establish any connection with the ventricles, but was lined by a thickened membranous layer of pia mater in which could be recognised scattered areas or flakes of grey matter. The left middle cerebral artery narrowed rapidly after giving off the anterior perforating branches, and could be traced to its further distribution only as a thread. The writer thinks that the lesions in the artery had occurred in the later months of foetal life, and was due to rupture of vessels in the placenta. The minute anatomy of the stem portion of the brain and of the spinal cord is detailed with considerable minuteness, and illustrated by many figures. WARRINGTON and MONSARRAT (xlvii.) describe certain *defects of the central nervous system* in a child aged 8 weeks, the subject of a healed lumbar spina bifida. The cerebellum was represented only by a few folia, the remainder with the peduncles being absent. No myelinated fibres entered it, and the transverse fibres of the pons and nuclei pontis were absent. The restiform body was hardly represented, the olives were entirely absent, as also were the external arcuate fibres, the superior cerebellar peduncles, the grey nuclei of the cerebellum, and the nuclei rubres tegmenti. The cord was symmetrically divided by an exostosis in the dorsal region into two parts. Medullated fibres were entirely absent from its lower portion ; in the upper part they were only found in Burdach's column and in the anterior ground

substance. REGNAULT (xlviii.) describes a case of a woman with two noses. The left had two nostrils and so had the right, but on this side the internal nostril was rudimentary. The writer positively puts forward the ridiculous explanation that the condition is the result of the fusion of two embryos, of each of which only one-half remains. LONGO (xlix.) narrates a case of *divided nose* in a child of 8 months. The left side was normal, but the right was a trumpet-shaped structure, the narrowest part of which was inserted between the inner canthus of the eye and the root of the nose. At the extremity of this tube was a small aperture through which air passed. WYNTER (l.) has recorded a case of *absence of nose and anterior nares* in a child æt. 6 weeks. There was no hare-lip or deficiency of the premaxilla. The hard palate was drawn up so as to simulate cleft palate, the soft palate was perfect. WATSON (li.) records and figures a case of cleft palate, hare-lip, and cleft nose in a child aged 3 months. HAMY (lii.) records a somewhat *similar case* in an adult Chinese male. The face was normal on the right side, on the left the entire of the internal incisive portion was wanting. BROECKAERT (liii.) adds some further cases to the examples of *congenital perfora-tions of the soft palate* which he had already published in Charles Bambeke's *Livre Jubilaire*, as recorded in an earlier report of this series. The instance here given is one of asymmetrical perforation of the posterior pillar of the fauces. A case of *branchial cleft persisting* may be noted from the *British Medical Journal* (liv.). BRADLEY (lv.) records two cases of *abnormality in the dentition of ruminants*. (a) Skull of a horse (lower jaw absent), seven cheek teeth on each side, a case of multiplication of serial organs. (b) Skull of anencephalous calf. The fronto-nasal process bore teeth with some resemblance to those of a camel. This may have been a reversion to an ancestor provided with a fuller complement of teeth than is present in the modern Bovidæ. GIUFFRIDA-RUGGIERI (lvi.) notes an instance of great *reduction in size of the ala of the sphenoid* in a Melanesian skull, an atrophic condition which was correlated with a marked antero-posterior enlargement of the squamous portion of the temporal bone. BIDONE (lvii.) describes a *pedunculated appendage*, fibro-muscular in character, which was found growing from the chin of a new-born child. ROHRER (lviii.), in a note on the relation between the formation of the auricle of anthropoid apes and certain congenital *malformations of the human auricle*, says that he has observed, amongst other anomalies, a cartilaginous strip passing from the crus helicis ascendens through the cymba in a rectangular direction to the point of bifurcation of the truncus antihelicis, which took origin on the upper side of the tragus on the incisura supratragica. This he believes to correspond to the crus anthelicis anterior described by Schwalbe in the ears of monkeys.

IV. THORAX.

HEITZ (lix.) describes a case of *congenital dilatation of the aorta*, which possessed four sigmoid valves, but only one coronary artery.

This vessel sprang from the interval between two of the valves and divided subsequently. KATZ (lx.) records a case of extreme *contraction of the aorta* immediately beyond the point at which the left subclavian artery is given off. Here it became so small in calibre that it was only just possible to insert a probe into it. The contracted portion was about 1 cm. in length, and opened into the ductus arteriosus, which was of considerable size. There was also a persistent foramen ovale. The child thus affected lived for three days. BOURLOT (lxi.) describes a heart in which there was a complete *absence of any connection between the pulmonary artery and the right ventricle*. At the point of its bifurcation the vessel was of normal size, but below this it became rapidly narrower and completely disappeared above the ventricle. Accompanying this condition were persistent foramen ovale, an aperture in the septum ventriculorum at the undefended spot, and persistent pervious ductus arteriosus. The right ventricle was much decreased in size. The child thus affected lived for three days. BRADLEY (lxii.) records a case of a *left superior* (anterior) *vena cava* which he observed in a dog. DASER (lxiii.) notes an *anomaly of the left vena innominata*, this vessel passing, to join the superior vena cava, behind the ascending aorta and in front of the right pulmonary artery. DE VECCHI (lxiv.) describes a *rare form of chorda tendinea* which ran from one of the cusps of the mitral valve to the wall of the ventricle near the aortic orifice. According to the author, only three similar cases have been recorded.

V. ABDOMEN.

ZANDER (lxv.) is the author of a case of *anus vestibularis* in a female æt. 20. Between the nymphæ were three openings—the meatus urinarius, which was normal, the introitus vaginæ, somewhat narrow, and, one-fifth of an inch further back, the opening of the intestine. This was surrounded by wart-like elevations of mucous membrane, and there was a distinct sphincter internus. A somewhat *similar case* is recorded by v. BARDELEBEN (lxvi.). M'ARTHUR (lxvii.) records a case of *imperforate anus* in which the rectal cloaca opened into the bladder. There was also external hermaphroditism. DURANTE (lxviii.) gives details of six cases of *congenital obstruction of the intestines*. Of these two were due to torsion, but in the remainder there were congenital defects. In two there was occlusion of the duodenum just below the place of entry of the bile and pancreatic ducts. In two there was occlusion of the small intestine, and in both of these cases the upper part of the gut formed a distended loop which lay in the left iliac fossa, the remainder being a thin cord. The author thinks that the theory which best explains the condition is that of the failure of the artery to the portion of intestine affected, the failure arising from contraction or obliteration of the vessel during intrauterine life. DUJARIER (lxix.) describes a case of *Meckelian*

diverticulum, where an artery from the superior mesenteric passed from the diverticulum to the parietal peritoneum, forming a band about 2·5 cm. long. The remarkable thing was that this artery was not contained in a mesentery, and the author thinks that its peritoneal clothing must have disappeared in the course of growth. ALTUCHOFF (lxx.) gives an account of an instance of unusually *long vermiform appendix*. The tube first passed upwards behind the cæcum, this part measuring 15·0 cm. in length. Then it bent to the left and downwards, and lay in the mesentery of the small intestine. This latter portion measured 10·0 cm. in length, and terminated in a bundle of fibrous tissue, well defined, which was 4·0 cm. in length. The appendix was 6 mm. in thickness. DURANTE (lxxi.) describes a case of congenital *adeno-myoma of the intestine*. There seems to be some possibility that this may have been an atrophic intestinal diverticulum. In the same subject there was also a supernumerary lobe to the liver about the size of a nut, and situated on the anterior aspect of the right lobe. JANICOT (lxxii.) gives an instance of *horse-shoe kidney*, which seemed to be made up of three renal elements, and occurred in a case of hydramnion. FRANCOIS-DANVILLE (lxxiii.) narrates two cases of congenital *anomaly of the kidney*: (*a*) absence of the organ on the right side; (*b*) small right kidney. Weighed 30 grms. as compared with 250, the weight of that of the left. LOEWENHARD (lxxiv.) describes an *ectopic right kidney*, which received arteries from the common and internal iliac arteries. The vein passed to the left common iliac. KATZ (lxxv.) describes a case of *absence of the penis*, in which there were a number of other malformations. There was no left kidney, and that of the right side presented the condition of congenital hydronephrosis. The left vas deferens opened into the right ureter, and there was no right vas deferens. The intestine opened into the bladder, and the urethra ended in a cul-de-sac below the symphysis pubis. There was a single umbilical artery, and the limbs presented various malformations. STAVELEY (lxxvi.) gives a series of instances of *abnormalities of the uterus*, met by him in practice, and chiefly of clinical interest. Other cases of uterine malformation which may be briefly mentioned are :—WARD (lxxvii.), *uterus didelphys*. KOSLENSKO (lxxviii.), *uterus bicornis* with twin pregnancy, one fœtus in either horn. KREVET (lxxix.), *uterus didelphys* with atresia vaginæ, but with no other malformations. GIRVIN and OSTHEIMER (lxxx.), further cases of a similar character. Of deficient development of the uterus the following cases may be mentioned :—GIROD (lxxxi.), *uterus unicornis*. The right horn was present, the left was detached and connected with the uterus at a point where the annexæ are usually found. HARLAN, a case of congenital *absence of the uterus* and the upper two-thirds of the vagina. The ovaries were present and embedded in the broad ligament.

VI. EXTREMITIES.

WITTFELD (lxxxiii.) consecrates an inaugural dissertation to the subject of *Sprengel's deformity*, viz., upward displacement of the scapula of one side. [*Note.*—Further references to the literature will be found in former reports of this series,—VIII. xlviii.–X. lxxxv.] A case of *Ectromelus* is detailed by M'GIBBON (lxxxiv.). The stumps of the lower extremities ended in fleshy nodules, but those of the upper were rounded as after amputation. Bones could be felt in all the stumps. There was no family history of malformations. AZOULAY (lxxxv.), a case of *Hemimelus*. The right hand consisted of a single finger, probably the index or 'medius, and there was apparently no carpus. On the left hand there were three fingers—pollex, index and medius. CONSTANTIN-DANIEL (lxxxvi.), a case of bilateral *absence of the radius*, complete on the right side, almost so on the left, with the distortion of the hand usual in such cases. The thumb in each hand was represented by a cutaneous appendage. FÉRÉ (lxxxvii.) describes a case of bilateral *absence* of the sterno-costal portions of the *pectoralis major*. HALLOPEAN (lxxxviii.) contributes the following notes of his dissection of a case of *congenital dislocation of the hip-joint* in a girl æt. 2½ years. The head of the femur was pointed, and owed this appearance to the flattening of its posterior aspect. The ligamentum teres was much elongated. The neck of the femur was short, and its angle nearly normal. As regards the innominate bone, the acetabulum was more open than usual, higher up on the bone and more posteriorly situated. Its articular surface was normal in shape, but it was very small. The secondary articular cavity was formed at the expense of the cotyloid ligament, which was enlarged and excavated at its upper part. A dissection of a case of the *same kind* but of much older standing is recorded by MORESTIN (lxxxix.). The femoral neck is greatly reduced in size—in fact, can hardly be said to exist—so that the mass, like an irregular mushroom, which represents the head of the bone, is sessile. It is flattened, very hard and smooth, but devoid of cartilage, and anteriorly more worn than at the back. The cavity in which the head was lodged was a new formation, developed on the external surface of the ilium by periosteal ossification. The acetabulum was covered by fibrous tissue; it was triangular at its upper part, and its posterior part was bent over the anterior so as to hide the base of the cavity. There was no cartilage in it, and no ligamentum teres. BOINET (xc.) records a case of *macrodactyly* of the middle finger of the right hand. As the radiograph well shows, this is not one of the ordinary cases where the increase in size is due to the soft tissues, but is one of actual gigantism of the bones. MORESTIN (xci.) narrates a case where there was a *post-minimus* on both hands and both feet of the same person. HOWE (xcii.) has made a study of the hexadactyle cat's foot, taking into consideration walking-pads, muscles, vascular and nervous structures, as well as the skeleton. Some facts suggest that the extra digit

occurs on the radial side, others point to the ulnar, but on the whole the balance of evidence points to the existence of the extra digit on the radial side of the three ulnar digits. PFITZNER (xciii.) records a case of bilateral *duplication of the fifth toe.* The left metatarsal was bifid, and each part carried a separate set of phalanges, two in the external toe, three in the internal. The right metatarsal was broader at its head than normal, but not bifid. It carried two sets of phalanges identical with those of the opposite side. MONRO (xciv.) has a case of congenital *deficiency of certain phalanges.* In the fore-fingers of both hands the second phalanges are absent. The proximal phalanx is normal. The terminal phalanx has the expanded basal portion longer and larger than usual. In the little finger, in the joint between the first and third· phalanges, on its outer side, a small wedge-shaped bone is interposed, partially dividing the joint. This wedge is probably the rudimentary secondary phalanx. The missing bone of the forefinger in all probability forms part of the enlarged base of the terminal phalanx. In the right foot the second phalanges are all rudimentary, and differ in size and shape from the normal. In the left foot the second phalanges are absent from the second and third toes. A cousin on the paternal side is said to have had a very short forefinger, but there is no other evidence of heredity. WALKER (xcv.) gives the genealogical table of a case of *malformation of the hand,* which extends over five generations. The malformation consists in the absence of one or more bones of the little and ring fingers, and absence of various joints between the phalanges, bony anchylosis accounting for the latter deficiency. KATZ (xcvi.) records the condition of *syndactyly* in a case where many other malformations were present, perhaps the most interesting and important being complete symblepharon in both eyes. There was also atresia ani, divarication of the pubic bones, so no symphysis, and pes varus of both sides. The child died immediately after birth. VOLKOV (xcvii.) has a contribution to the literature of *supernumerary bones of the foot— and triphalangy.* He especially refers to the os trigonum, external tibial bone (*i.e.* detached scaphoid tubercle), secondary cuboid, double first cuneiform, and intermetatarsal bone. He concludes, (*a*) The first metatarsal (or first metacarpal) may be considered to be—as it was— the first phalanx. (*b*) The first cuneiform (or the trapezium) may be considered as the first metatarsal (or metacarpal) reduced. (*c*) The tubercle of the scaphoid in man or the external tibial (or external radial) in rodents may represent the vestige of the first cuneiform (trapezium). (*d*) The bones known under the name of prehallux or precuneiform are probably only the more or less transformed sesamoids of the first metatarsal (first metacarpal), or of the first cuneiform (trapezium) of the actual nomenclature. DWIGHT (xcviii.) describes three *feet with accessory ossicles* :—(*a*) Os intercuneiforme. This seems to be described for the first time. It lies on the dorsum of the foot, in a fossa between the proximal ends of the first and second cuneiform bones. (*b*) Intercuneiforme and calcarius secundarius. (*c*) Para-cuneiform, possibly a pathological structure. Lies at the base of the

internal cuneiform, and between it and the scaphoid on the dorsum of the foot. In this case there was also a calcaneus secundarius.

RAUBER (xcix.) notes a case in which on both sides of the body there were present an os styloideum carpi and a supra-condylar hook on the humerus. RAUBER (c.) also contributes a note on the os styloideum carpi ultimale, with an account of its internal structure.

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lxxviii. *Centralbl. f. Gynäk.*, 1902, 2.

lxxix. *Zeits. f. Geb. u. Gyn.*, xlvi. 39.

lxxx. *Amer. Journ. of Obst.*, xlv. 782, 785.

lxxxi. *Bull. Soc. Anat. de Paris*, 1901, 665.

lxxxii. *Cin. Lancet and Clinic.*, Jan. 25, 1902.

lxxxiii. *Inaug. Diss. Bonn.*, 1901.

lxxxiv. *Lancet*, Sept. 20, 1902.

lxxxv. *Bull. et Mém. de la Soc. d'Anthrop. de Paris*, 1902, 51.

lxxxvi. *Bull. Soc. Anat. de Paris*, 1902, 360.

lxxxvii. *Journ. de l'Anat. et de la Phys.*, 1901, 540.

lxxxviii. *Bull. Soc. Anat. de Paris*, 1902, 289.

lxxxix. *Ibid.*, 1901, 612.

xc. *Presse Médicale* (date not known).

xci. *Bull. Soc. Anat. de Paris*, 1902, 64.

xcii. *American Naturalist*, xxxvi. 427.

xciii. *Zts. f. Morph. u. Anthrop.*, Bd. iv. hft. ii. s. 380.

xciv. *Brit. Med. Journ.*, Apr. 26, 1902.

xcv. *John Hopkins Hosp. Bulletin*, xii. 121.

xcvi. *Bull. Soc. Anat. de Paris*, 1901, 485.

xcvii. *Bull. et. Mém. de la Soc. d'Anthrop. de Paris*, 1902, 274.

xcviii. *Anat. Anzeiger*, xx. 465.

xcix. *Ibid.*, xxi. 263.

c. *Ibid.*, xxii. 210.

(The reporter wishes to express his acknowledgments to the abstracts in the *British Medical Journal* and *American Journal of Obstetrics* for some of the above.)
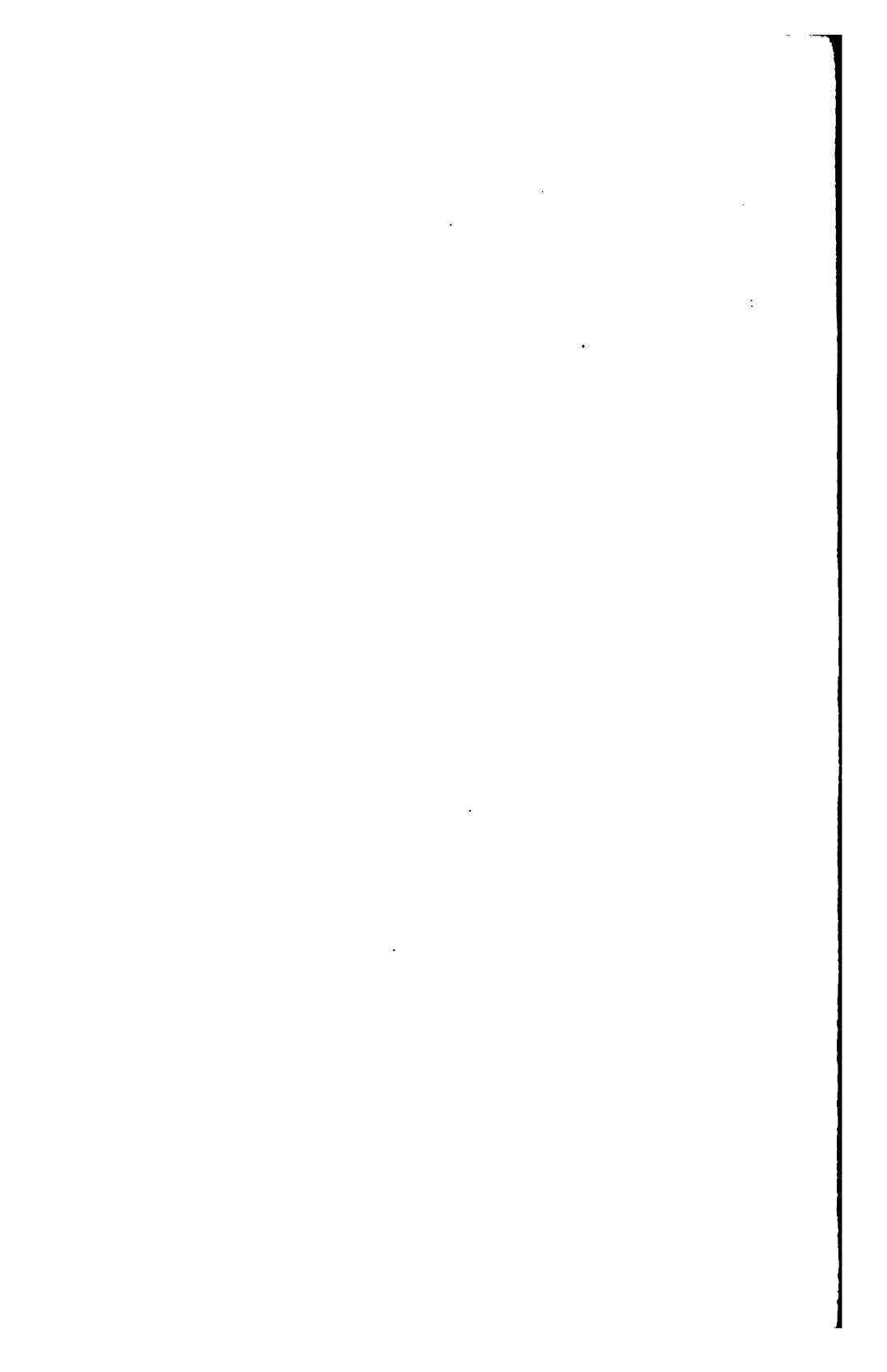
Journal of Anatomy and Physiology.

ON THE MEANING OF SOME OF THE EPIPHYSES OF THE PELVIS. By F. G. PARSONS, *Lecturer on Human and Comparative Anatomy at St Thomas's Hospital.*

IN the *Morphologisches Jahrbuch* are two very interesting papers by Dr Ernst Maynert [1] dealing with the epipubis and hypoischium of Reptiles, in which he points out that these structures are formed in the mid ventral line, and probably are, in the first instance, independent of the rest of the pelvis. It is to the fate of these structures in the Mammals that I wish to call attention, but, before doing so, I must make a few remarks about the reptilian arrangement.

With regard to the hypoischium, Maynert shows what a variety of forms it may take, sometimes being specially elongated, sometimes almost entirely suppressed, sometimes bifid at its pelvic end, at others toward the cloaca, sometimes fully ossified, sometimes entirely cartilaginous, but always forming a more or less perfect support for the anterior lip of the cloacal orifice, and earning its alternative name of ' Os cloacæ.'

Of all the reptilian pelves which I have examined, I think perhaps that of the Sphenodon Lizard (fig. 1) will give the fairest idea of this structure. It (the hypoischium) is attached anteriorly between the junction of the two ischia which are uniting to form the ischial symphysis so common in Reptiles ; if it is carefully examined, it will be seen to continue forward between the two ischia and then to reach the interval between the two pubes, anteriorly to which it expands to form a diamond-

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[1] " Ueber die Entwicklung des Os Hypoischium, Os Epipubis und Ligamentum medianum pelvis bei den Eidechsen," *Morph. Jahr.*, 1891, p. 123 ; " Untersuchungen über die Entwicklung des Beckengürtels der Emys lutaria taurica," *Morph. Jahr.*, 1890, p. 537.

shaped plate of cartilage which is now called the epipubis. In the specimen from which my figure was drawn, there was a bilateral attempt at ossification in the epipubis, and to a less extent in the hypoischium; but the point which I want specially
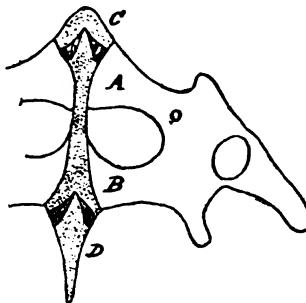
FIG. 1.—Pelvis of Sphenodon Lizard. *A*, pubis; *B*, ischium; *C*, epipubis; *D*, hypoischium. In this and the following diagrams the cartilage is dotted and the bony epiphyses shaded.

to call attention to is that the epipubis and the hypoischium form a continuous cartilaginous element in the mid ventral line.

In the pelvis of the Crocodiles the hypoischium is not a distinct rod as it is in the Lizards, but in the fresh state (fig. 2)
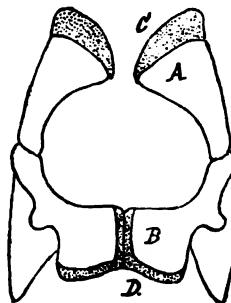
FIG. 2.—Pelvis of young Alligator. *A*, pubis; *B*, ischium; *C*, epipubis; *D*, hypoischium.

the cartilage which forms the symphysis ischii, when it reaches the hinder end, is continued outward from the mid line along the caudal margin of the ischium, and approaches the condition of things which I mean to deal with next.

We now leave the Reptiles for the Mammals, and in these Maynert says that he found a bone like a hypoischium in eleven species, nine of which belong to the order of Marsupialia, the other two being the Pangolin (Manis, once called Pholidotus) and the Beaver (Castor).   I can quite agree with his statement that the bone is here, and to my mind it seems evident that not only is it *like* the hypoischium, but that it *is* the hypoischium.   I have, through the kindness of Prof. Stewart and Mr Oldfield Thomas, been able to examine all the pelves in the College of Surgeons and Natural History Museums, and certainly the Marsupials are the most instructive.   If the pelvis of quite a young
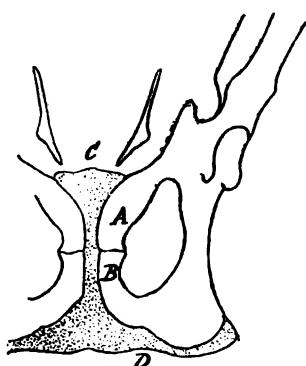
FIG. 3.—Pelvis of young Kangaroo.   *A*, pubis ; *B*, ischium ; *C*, epipubis ; *D*, hypoischium.

Kangaroo, for example, is examined, it will be seen that the symphysis is ischio-pubic (fig. 3), and not altogether pubic as in Man ; consequently the hind part is formed by the ischium of each side very much as in Sphenodon.   In addition to this there is the same tract of cartilage that was seen in Sphenodon connecting the pubes and ischia of opposite sides, while behind (caudad) the symphysis this cartilage forms a triangular plate filling up the subpubic or, to be more accurate, the hypoischial angle, and reaching outward as far as the tuberosity of the ischium on each side.   At the anterior (cephalic) end of the symphysis the cartilage expands somewhat and forms a triangular plate corresponding exactly in position with the epipubis of Sphenodon.

In an adult Kangaroo's pelvis (fig. 4) all the part behind the symphysis becomes ossified and forms a triangular bony plate, the lateral angles of which stretch outward as far as the tuberosity of the ischium, while the part in front of the pubis also ossifies and forms a small triangular bony plate which corresponds entirely with the epipubis. These bones can hardly be spoken of as epiphyses, since in quite adult Kangaroos they are ununited with the rest of the pelvis, and I doubt whether the hypoischium ever unites with it, though of this I cannot be sure.

If an intermediate stage, in which the ossification is in progress, be next examined, the bone will be seen to be
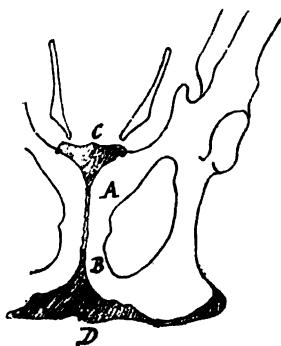
Fig. 4.—Pelvis of adult Kangaroo. *A*, pubis; *B*, ischium; *C*, epipubis; *D*, hypoischium.

deposited in two or even three centres in each half of what I may provisionally speak of as the hypoischium (fig. 5); one centre appears on each side near the middle line and in very much the same position in which the centres appear in Sphenodon, another forms a cap over the dorsal part of the tuberosity of the ischium, while occasionally there may be a third one between the two. With regard to the ossification of the epipubis, I have not been fortunate enough to see how the bone first appears, but I have little doubt that it is deposited symmetrically as in Sphenodon; indeed, I think it is very doubtful whether in the whole vertebrate skeleton there is such a thing as a true median centre of ossification. I am not, however, so much concerned with the way in which the first bony

deposits are laid down as to establish the great likelihood that the cartilaginous layer in the young Marsupial is the same morphological element as the epipubis and hypoischium of the Reptile as shown in Sphenodon. If this is granted, it matters little, I think, how the bone is deposited; it may be by one centre on each side in one animal, and by two or three in another, depending largely on the length of the cartilaginous strip which has to be changed into bone. Against the theory that this cartilaginous strip of the marsupial pelvis is the reptilian epipubis and hypoischium, I have only as yet heard one objection from the morphologists I have talked to on the
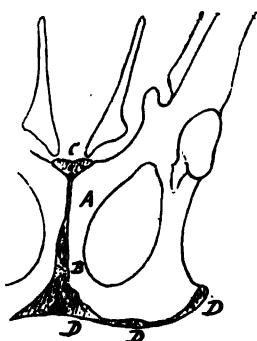
FIG. 5.—Pelvis of young Wallaby. *A*, pubis ; *B*, ischium ; *C*, epipubis ; *D, D, D*, separate ossifications in the hypoischium.

subject; some of them have a general objection to homologising any mammalian epiphysis with that of Reptiles, because the latter are said to have no epiphyses to their long bones. I am, however, convinced that this is an erroneous belief. It is quite easy to prove that epiphyses are common in Reptiles though they are not so numerous as in Mammals.

In the Monotremes Maynert says that he has failed to find any trace of the hypoischium and epipubis; I feel fairly sure, after examining many specimens of Ornithorhynchus, that in that animal, at least, they are present, but they fuse very early and very completely with the rest of the pelvis, and in this way differ markedly from the similar marsupial structures. In the Rodents (fig. 6) and Ungulates the hypoischial element is quite distinct, and the symphysis is still ischiopubic, but the ossi-

fication of the hypoischium does not quite unite with its fellow
of the opposite side in the middle line, and so no triangular
plate of bone is found as in the Kangaroo. The reason for this
doubtless is that the young of these animals are born in a more
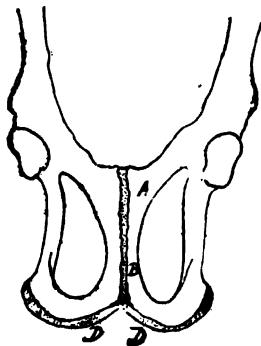
FIG. 6.—Pelvis of Viscacha. *A*, pubis ; *B*, ischium ;
D, D, hypoischium.

developed state than are the marsupial young, and it is necessary
that the symphysis should be able to gape somewhat during
parturition.

When we come to the pelvis of Man we have to deal with
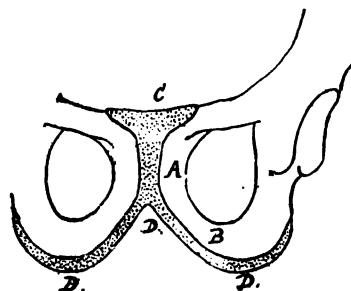
FIG. 7.—Human pelvis at twelve years of age. *A*, pubis ;
B, ischium ; *C*, epipubis ; *D*, hypoischium.

a pubic symphysis only, otherwise at about twelve years of
age (fig. 7) the likeness to the marsupial and reptilian arrange-
ment is striking. There is a continuous edging of cartilage,
which begins as a little cap over the pubic spine, lines the

crest, angle, and symphysis, and then runs along the subpubic
arch as far as the tuberosity of the ischium, for which it forms
a well-marked cap. This, I have no doubt, is the same structure
as that of the young Kangaroo, and represents the continuous
epipubis and hypoischium of the Reptile.[1]

Ossification begins at the two ends of this cartilaginous
edging, but there may be more than one deposit in each place.
In the College of Surgeons Museum there is the pelvis of a
boy of 14 which shows (fig. 8) the presence of two
deposits of bone beneath the tuberosity of the ischium, and
one smaller at the angle of the pubis. At 16 there is a com-
plete bony cap for the tuberosity of the ischium, which quickly
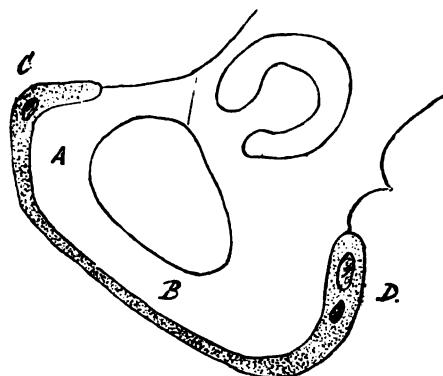
FIG. 8.—Human os innominatum at fourteen years of age. *A*, pubis ;
B, ischium; *C*, epipubis ; *D*, hypoischial ossification.

creeps along the cartilaginous edging, and about 20 (fig. 9) has
ossified that edging as far as the point of union of the rami
of the pubis and ischium—that is to say, it goes morphologically
as far as it does in the Kangaroo, in which the symphysis is
ischio-pubic. I think that I have now said all I can in support
of my belief that the hypoischium of the Reptile explains the
presence of the epiphysis of the tuberosity of Man's ischium.
With regard to the epipubis, it is interesting to notice that in

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[1] In Sphenodon these two elements are directly continuous by cartilage, but
in many other Lizards the part between the pubic symphysis and that of the
ischium is often converted into a median ligament, owing to the fact that the
two symphyses are far apart.

the young human subject the cartilaginous border runs outward
as far as the pubic spine, and so with its fellow of the opposite
side forms a triangular plate very like the epipubic bone of
the Marsupial.

The first deposit of bone is, as I have shown, and as Thomson
also notices,[1] at the angle of the pubis, and so closely cor-
responds with the centre in the epipubis of Sphenodon. Later
on this ossification creeps downward as a thin scale along the
pubic symphysis and also outward along the crest of the pubis
as far as the pubic spine. Sometimes a small distinct deposit
is said to appear for the pubic spine, and this may be looked
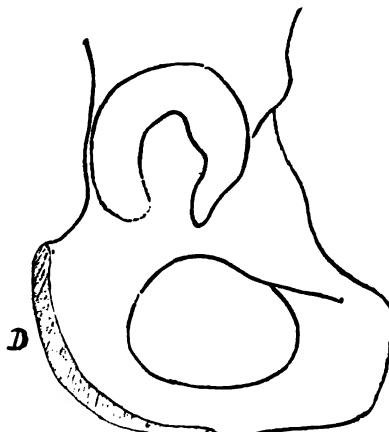
Fig. 9.—Human os innominatum at twenty years of age.
D, hypoischial epiphysis.

on as a disappearing remnant of the marsupial bone which
Wiedersheim regards as part of the epipubis. I have never
been fortunate enough to see this centre, but one point which
makes me a little doubtful of its homology with the marsupial
bone is the fact that the spine of the pubis is quite a human
characteristic, and is apparently a physiological result of the
pull of Poupart's ligament. In the lower Mammals Poupart's
ligament as a definite structure can hardly be said to exist.

[1] Cunningham's *Text-Book of Anatomy*, p. 213. Thomson gives the date of the
appearance of this epiphysis as 18 years. The specimen in the R. C. S. Museum
which I quote shows that it may come four years earlier.

The only other pelvic epiphysis of which I wish to speak at present is that for the anterior inferior spine of the ilium, and I do so because it makes such a sharp contrast with those with which I have been dealing. Although I have now looked at the pelves of very many young Mammals, I have never yet found this epiphysis in any other animal than Man. When a new structure is met with in Man, one is always inclined to seek an explanation in the erect position, and here I think a clue may be found. In Man the straight head of the rectus is much stronger than in other Mammals, and, from the position of the limb, pulls harder on the bone; and I think that the anterior inferior spine is one of those traction epiphyses, nearly akin to sesamoid bones, which so often come where a strong pull has to be met. In this, if I am right, it is like the spine of the pubis or the lesser trochanter, and greatly differs from the epiphysis of the ischial tuberosity which leads us back to reptilian days, or from that of the symphysis pubis which goes still farther back to the tailed Amphibia.

ON THE SO-CALLED 'GYRUS HIPPOCAMPI.' By G. Elliot Smith, M.A., M.D., *Fellow of St John's College, Cambridge; Professor of Anatomy, Egyptian Government School of Medicine, Cairo.*

In a recent number of this *Journal*[1] I called attention to the fact that the true pallium really consists of three morphologically distinct parts:—hippocampus, lobus pyriformis, and neopallium. The latter presents the utmost contrast to the other two pallial areas, not only in its histological structure and physiological characters, but more especially in regard to its behaviour in the mammalian series. This can be expressed in a word by saying that the neopallium is eminently progressive, whereas the hippocampus and pyriform lobe are stationary or even actually retrogressing in the recent Mammalia.

If the validity of this mode of subdividing the pallium be admitted, we must of necessity discard as useless and confusing the terms 'gyrus hippocampi' and 'gyrus uncinatus,' because the area so-called is composed partly of neopallium (fig. 1, 'paradentate gyrus') and partly of pyriform lobe, with the addition of small areas of·hippocampus (fig. 2, *a* and *b*) and nucleus amygdalæ (*n.am.*). The latter is a large ganglionic mass which does not strictly belong to any of the three pallial areas: it is continuous above with the corpus striatum, in front with the locus perforatus, behind with the hippocampus, and below with the pyriform lobe: a small part comes to the surface, and it is, I believe, not generally recognised that the structure which Gustav Retzius (*op. cit. infra*) calls '*gyrus semilunaris*' (in the human brain) and '*gyrus lunaris*' (in the brains of other mammals) is nothing else than this exposed part of the nucleus amygdalæ (figs. 1 and 2, *n.am.*).

It is quite unnecessary to give a full account of this region, because Retzius[2] has described it in great detail, and in an earlier memoir[3] I have called attention to its salient features.

[1] Vol. xxxv., July 1901, "Notes upon the Natural Subdivision of the Cerebral Hemisphere," pp. 431-454.

[2] Gustav Retzius, *Das Menschenhirn*, Stockholm, 1896.

[3] "The Relation of the Fornix to the Margin of the Cerebral Cortex," This *Journal*, vol. xxxii., 1897, p. 29.

That the region labelled 'pyriform lobe' really represents the posterior part of the lobus pyriformis is abundantly shown, not only by its histological features, but also by a comparison of the human organ with other mammalian brains. This fact has been very clearly demonstrated by Retzius,[1] and I have recently shown how the pyriform lobe in the Primates becomes gradually modified in form, from a condition exactly comparable to that of most mammals to the human-like form of the lobe found in the Gorilla.[2]

The pyriform lobe in the human brain extends backward as
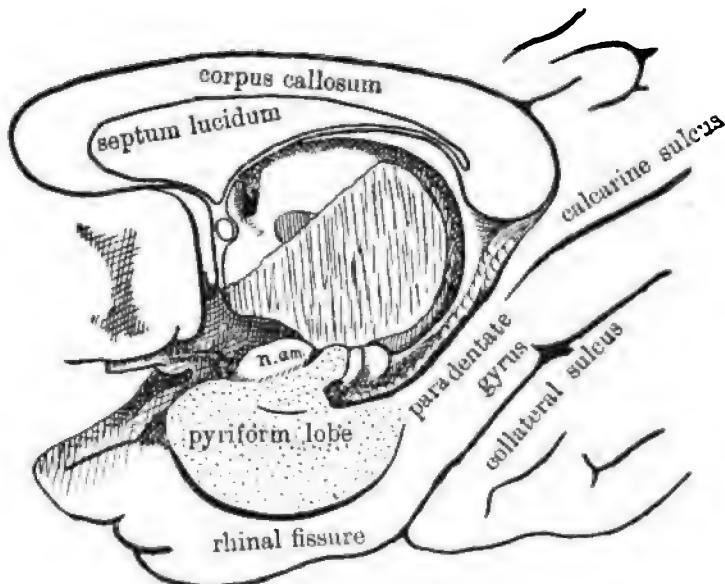
FIG. 1.—Part of the mesial surface of the right cerebral hemisphere of a Fellah, ♂, æt. 62 ann., nat. size.

far as a point opposite the tip of the uncus (which is formed of a little knob (b) of inverted hippocampus which Retzius calls 'gyrus intralimbicus').

The chief reason why the pyriform lobe has not hitherto been

[1] Gustav Retzius, " Zur äusseren Morphologie des Riechhirns der Säugethiere und des Menschen," *Biologische Untersuchungen*, Bd. viii. No. 2, Stockholm, 1898.

[2] *Descriptive and Illustrated Catalogue of the Royal College of Surgeons*, second edition, vol. ii., 1902. See especially p. 441.

generally recognised in the human brain is that the rhinal fissure, which delimits this area, is subject to so much irregularity that its identity has not been appreciated by most writers. In fact, Retzius is the only writer, so far as I am aware, who has recognised the full extent of the rhinal fissure in the human brain. The typical form of this fissure, such as is exhibited in the brain of the Apes, is not often seen in the European brain, but that it does sometimes occur is shown by Retzius.[1] The latter writer also shows the characteristically
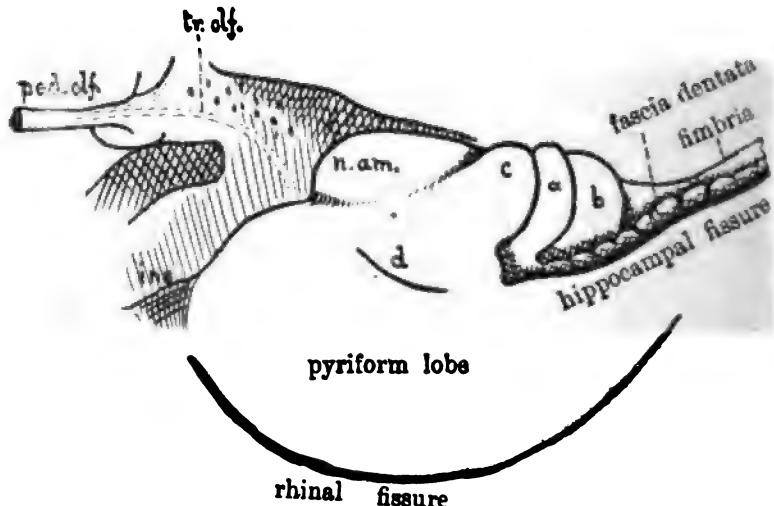
FIG. 2.—Part of fig. 1 enlarged. *a*, the 'benderella' of Giacomini, *i.e.*, the anterior (lower) extremity of the fascia dentata; *b*, the tip of the uncus, composed of alveus-coated inverted hippocampus; *c*, dorsal tongue-like process of the pyriform lobe; *d*, a very constant furrow on the pyriform lobe; *n.am.*, exposed part of the nucleus amygdalæ; *tr.olf.*, external olfactory tract; *ped.olf.*, the posterior part of the pedunculus olfactorius; *inc.*, incisura temporalis (part of the rhinal fissure).

mammalian form of complete rhinal fissure exhibited in the human fœtus.[2]

The primitive form of rhinal fissure (see the figure) occurs much more often in the brains of Egyptians and Abyssinians than it does among Europeans, and among the Soudanese races it is of common occurrence.

In the European brain, however, the posterior part of the

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[1] *Menschenhirn. Vide* Tafel lx., *inter alia.*   [2] *Op. cit.*, Tafel xxxii. fig. 2.

fissure usually becomes separated from the incisura temporalis (fig. 2, *inc.*), and often becomes confluent with the sulcus collateralis.[1] In fact, most writers have come to regard this caudal part of the rhinal fissure as the anterior part of the collateral sulcus. To understand how unfounded such an idea is, I need only recall the fact that the rhinal fissure is, next to the hippocampal fissure, the oldest furrow on the surface of the hemisphere and the common property of all mammals (not excluding even the Monotremata); whereas the collateral sulcus is a recent formation which is only properly developed in the higher Primates.[2]

The wide range of variation and distortion of the rhinal fissure which occurs in the human brain is admirably shown in the beautiful series of plates in Retzius' great work.

For the reasons stated above it is desirable to separate the 'pyriform' part of the uncinate gyrus from the non-pyriform or neopallial part. The neopallial part of the gyrus cannot then be named 'uncinate,' because the whole region of the uncus is excluded. In addition, it is highly undesirable to perpetuate the use of the term 'hippocampal' in reference to this convolution. Such a usage has in the past been the cause of an immense amount of confusion in the literature of Comparative Anatomy. Very many anatomists, including the most prolific writers on Comparative Neurology in Europe and America, constantly fail to draw any distinction between the hippocampus (cornu Ammonis) and the 'hippocampal gyrus' (which is part of the neopallium); and the result of this is the most hopeless misunderstanding. As this is wholly due to the similarity of the names, I propose to discard the term 'hippocampal gyrus,' and to call the neopallial part of the uncinate convolution by the name '*gyrus paradentatus*,' in reference to the fact that it pursues a course parallel to the fascia dentata, from which it is separated by the hippocampal (dentate) fissure.

Nor does it seem desirable to retain the term 'gyrus uncinatus' in reference to the anterior (rhinencephalic) part of the convolution. For one reason, an essential part (fig. 2, *a*

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[1] *Vide*, for example, *Menschenhirn*, Tafel lxxv. fig. 4.

[2] "On the Homologies of the Cerebral Sulci," This *Journal*, vol. xxxvi., 1902, pp. 309–319.

and *b*) of the hook (*uncus*) is hippocampal, and therefore ought
to be considered as part of the hippocampus, and not be grouped
with the pyriform lobe. On the other hand, it would be a
distinct gain, not only to Comparative but also to Human
Anatomy, if the region which is homologous to the pyriform
lobe of other mammals were called by the same name in the
human brain. If it be objected that the use of the term 'lobe'
might lead to some confusion (because the human brain is
already conventionally divided into 'lobes'), the term '*area
pyriformis*' might be employed to indicate that region of the
human brain which represents the posterior (postsylvian) part
of the pyriform lobe of other mammals.

The so-called 'uncinate' or 'hippocampal' gyrus thus becomes
split up into four separate areas:—paradentate gyrus, area
pyriformis, nucleus amygdalæ, and a hippocampal part.

It may be asked why the term 'gyrus' is not applied to the
pyriform area. I have intentionally refrained from using this
expression, because every gyrus in the cerebral hemisphere will
then be a part of the neopallium—a distinction which seems
worthy of being maintained. If, however, we were to follow
some writers who call the fascia dentata a 'gyrus,' there would
then be no reason why the pyriform area should not also be
so called. Gustav Retzius, in fact, applies the term equally to
the neopallium and the rhinencephalon. Nothing is gained by
such a use of the term gyrus, whereas a useful distinction is
maintained if this word is applied only to the neopallium.

It must be remembered that the area we have been consider-
ing includes only the posterior part of the pyriform lobe. The
anterior part (as in all the Apes) dwindles to very small pro-
portions, and its situation is indicated merely by the lateral
olfactory tract (fig. 2, *tr.olf.*), which passes backward from the
olfactory peduncle (*ped.olf.*), skirts the lateral border of the
locus perforatus, and, after crossing the deep vallecula Sylvii,
reaches the surface of the posterior part of the pyriform lobe.

None of the facts brought forward in these notes are new.
The suggestions which I have made give expression to the
teaching of Comparative Anatomy, which has too long been
ignored in the domain of Human Anatomy.

NOTES ON THE MORPHOLOGY OF THE CEREBELLUM.

By G. ELLIOT SMITH, M.A., M.D., Ch.M., *Fellow of St John's College, Cambridge ; Professor of Anatomy, Egyptian Government School of Medicine, Cairo.*

IN a short memoir published in this *Journal* last year[1] I briefly explained the mode of subdivision and the nomenclature of the cerebellum which I had adopted in three works dealing with the brain in every mammalian Order.[2]

In the first of those three monographs I explained at some length the urgent need for some mode of subdividing the cerebellum other than that adopted in Human Anatomy, which is altogether unsuitable, and in most cases quite inapplicable, in Comparative Anatomy.

The earlier investigations of Kuithan and Stroud had shown that in three such diversely-specialised and widely-separated mammals as *Ovis, Felis,* and *Homo* the chief fissures of the cerebellum develop in the same manner; and my examination of the brain in practically every existing genus of the Mammalia showed these same fissures to be distinguished by their depth and constancy.

I attempted to draw up a scheme of subdividing the organ, based upon the recognition of the facts demonstrated by these two lines of investigation.

The only region presenting any difficulty was that including the connecting strands of grey matter which link the floccular lobe to the 'vermis.' Neither Stroud nor Kuithan had discussed the nature of this connection ; but I discovered that " in the smallest representatives of every Order—as, for example, *Perameles, Dasyurus, Trichosurus,* and most Marsupials, in all Insectivores and Chiroptera, in most Rodents, in the Dasypodidæ, in *Procavia* of the Ungulata, and in such Lemuroids as *Tarsius*

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[1] " The Primary Subdivision of the Mammalian Cerebellum," This *Journal,* vol. xxxvi., July 1902, pp. 381-385.

[2] (*a*) " The Brain in the Edentata," *Transactions of the Linnean Society of London,* vol. vii. part vii., 1899 ; (*b*) *The Descriptive and Illustrated Catalogue of the Royal College of Surgeons of England—Physiological Series,* 2nd edition, vol. ii., 1902 ; (*c*) " The Morphology of the Brain in the Mammalia—with Special Reference to the Lemurs," *Transactions of the Linnean Society of London,* vol. viii. part 10.

and *Microcebus*—there is a simple undivided band joining the dorsal paraflocculus to the pyramid" [*op. cit. supra*, (1), p. 384]. The pyramid is the lowest (most caudal) lobule of the region I called the 'middle lobe,' and is separated from the uvula (which is the uppermost lobule of the 'posterior lobe') by the fissura secunda (which probably corresponds to the 'prepyramidal fissure' of Human Anatomy).
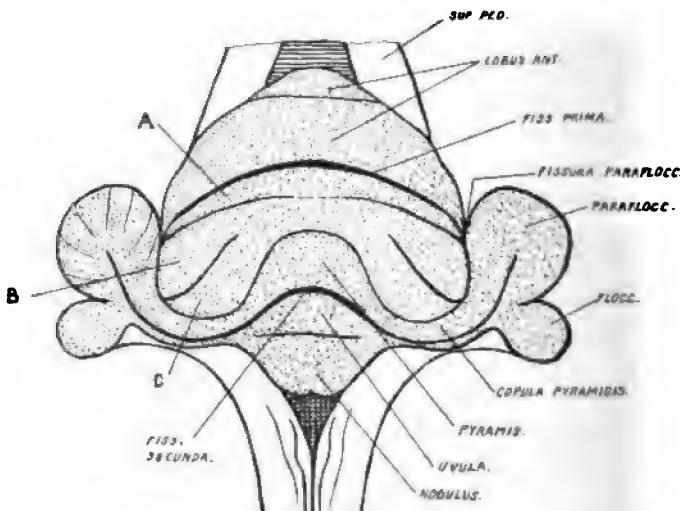
FIG. 1.—Diagram to represent the fundamental subdivisions of the cerebellum spread out in one plane.

In a recent number of this *Journal*[1] a thinly-veiled attack has been made on my position in regard to this matter by a writer, who shows a singular reluctance to add point to his observations by referring in any way to the offending statements. Yet it is clear that this question of the relation of the paraflocculus to the vermis is the *raison d'être* of that document, because all the other matters discussed merely exemplify, in the case of the Rabbit, the fundamental structure of the cerebellum, which the researches of Kuithan, Stroud, and the writer have shown to prevail in all the Placentalia.

We are told [*op. cit.*, (3), p. 121] that in the adult Rabbit it is

[1] "On the Development and Homology of the Mammalian Cerebellar Fissures," This *Journal*, vol. xxxvii., January 1903, pp. 112-130.

the uvula ('lobe D') which is joined to the paraflocculus; and " the ground upon which his statement is based " is that it does so in the Hare's cerebellum! The author then proceeds to state that the uvula ('lobe D') is "confined to the vermis" (*i.e.*, is *not* joined to the paraflocculus) in *Erinaceus* (p. 123), *Mus* (p. 125), *Arvicola* (p. 125), and *Pteropus* (p. 126), and from these data formulates the illogical general conclusion that the uvula ('lobule D,' *i.e.*, the upper part of 'lobe D,' which is equivalent to the uvula) *is* joined to the dorsal limb of the paraflocculus (p. 128). In other words, the author of this generalisation
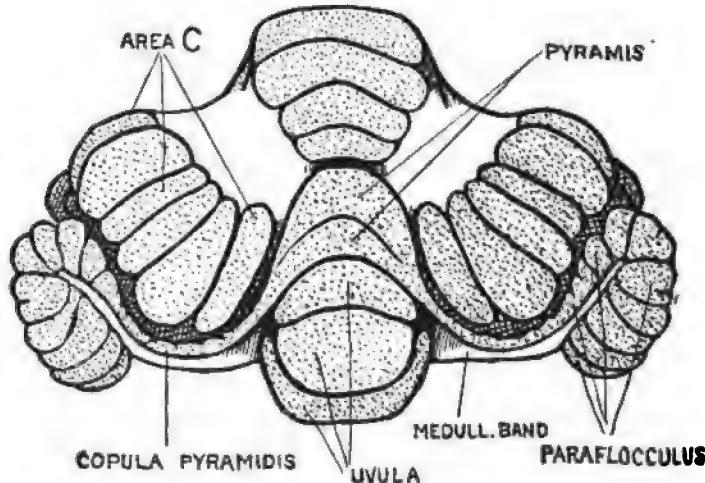
Fig. 2.—The caudal aspect of the cerebellum of a Rabbit (*Lepus cuniculus*). × 3½.

places the evidence of a (presumably anomalous) Hare's brain in opposition to his own statements concerning the condition in *Erinaceus, Mus, Arvicola*, and *Pteropus*, not to mention the evidence which I have collected in the four memoirs quoted above.

I have examined the structure of the cerebellum in a large number of Rabbits in reference to this disputed point. In the majority of these I have found the condition represented in the accompanying drawing (fig. 2). The narrow dorsal limb of the paraflocculus is joined by means of a long, narrow, wrinkled band of grey substance (copula pyramidis) to the pyramid, of which two broad folia are usually exposed on the surface. In

most cases the upper margin of this copular band is very sharply delimited from the (other) folia of the area C by a deep fissure continuous with that bounding the pyramid on its dorsal aspect. But in some cases the upper folium of the pyramid becomes continuous with the folia of area C—an arrangement which invariably occurs in the Apes (including both Cebidæ and Cercopithecidæ). In one case the lateral extension (copula) of the pyramid did not reach so far as the paraflocculus. In no case, however, did the copular band (or any other parafloccular link of grey substance) join the uvula. In fact, among the very large series of mammalian brains which I have examined in regard to this particular feature during the last five years, I have seen a (macroscopic) cortical connection between the paraflocculus and the uvula only in the human brain and in single anomalous specimens of fœtal *Trichosurus* and *Bos.*

When I was writing my short abstract (*op. cit. supra*) last year I carefully examined a complete series of sagittal sections through the brain of *Notoryctes*,[1] which possesses a simpler cerebellum than any other mammal.[2] In that organ I found a narrow band of cerebellar cortex (which was quite invisible to the naked eye) lying below the copula pyramidis (fig. 1): it was continuous mesially with the cortex of both uvula *and nodulus*, and laterally with the flocculus and the *ventral* part of the paraflocculus. It occupied, in fact, the same position as the medullary band (fig. 2), visible to the naked eye in most other mammals. This, however, cannot be the structure referred to in the critique quoted above, because a macroscopic cortical band passing to the *dorsal* limb of the paraflocculus from the uppermost lobule (only) of the uvula is meant.

In my notes published in this *Journal* last year (*op. cit. supra*, vol. xxxvi. p. 384) there is an important misprint. I referred to the fissura horizontalis magna as separating the areas A and B, but as the context clearly shows it is the furrow between the areas B and C (fig. 1).

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[1] Five specimens of this interesting Marsupial were generously placed at my disposal by Professor Baldwin Spencer of Melbourne, whom I desire to thank for his valuable gift.

[2] The only fissures crossing the middle line in this curious little organ are the fissura prima, the fissura secunda and the cleft separating the uvula and nodulus.

A PRELIMINARY COMMUNICATION ON SOME CEPH-ALOMETRIC DATA BEARING UPON THE RELA-TION OF THE SIZE AND SHAPE OF THE HEAD TO MENTAL ABILITY. By Dr REGINALD J. GLADSTONE, F.R.C.S., *Senior Demonstrator of Anatomy, Middlesex Hospital, London, W.*

A LARGE amount of laborious and painstaking work has been undertaken, both recently and in times which may be regarded as historical, with the view of determining the relationship, if any, between different types of head and various mental characteristics or degrees of ability. The results of this labour appear, until the last ten or fifteen years, to have been some-what indefinite and often contradictory.

Some of the older physiognomists and phrenologists, and notably Lavater and Gall, attained a high degree of proficiency in estimating the character and disposition of individuals, by means of a careful observation of external features, and their published works are not only of great interest, but contain also valuable scientific data. The conclusions drawn by others, however, were for the most part founded upon hypotheses rather than on observations, and are of little value to the psychologist.

Recently articles have appeared also in some of the popular journals which are based on materials furnished by hat manu-facturers, and which are illustrated by remarkable tracings which are said to have been taken by the 'hatter's machine' for recording the outline of the head; these are interesting, but for the most part absolutely untrustworthy. One table of figures, which has been compiled by a well-known straw-hat manufacturer, and for which I am indebted to the kindness of Mr A. Pearce Gould, for whom it was originally drawn up, is of considerable interest, and I venture to introduce it here, for the purpose of showing how easily mistakes may arise from these kind of data, however carefully they may be formulated.

The table shows the relative frequency of various specified sizes of straw-hat supplied for the use of boys and men in the years 1868 and 1901–2. The figures have been averaged from a large number, and reduced in each case to two dozen.

TABLE I.

Size of hat— Length, . Circumference,	6" 18⅞"	6⅛" 19¼"	6¼" 19⅝"	6⅜" 20"	6½ 20⅜	6⅝" 20¾"	6¾" 21¼"	6⅞" 21⅝"	7" 22"	7⅛" 22⅜"	7¼" 22¾"	7⅜" 23¼"	7½" 23⅝"
Boys, 1868, .	...	...	1	3	5	6	5	3	1	=	2 dozen		...
,, 1901-2, .	...	1	3	6	6	5	3	...	...	=	2 dozen		...
Men, 1868, .	...	...	...	...	...	1	3	5	· 5	4	4	2 = 2 dozen	
,, 1901-2, .	...	...	...	...	3	5	7	6	2	1	...	= 2 dozen	

This table shows a marked decrease in the sizes of hat which were supplied in the year 1901-2 as compared with the sizes which were sold in 1868, both in boys and men. If during this period there had been a diminution in the size of the men's heads, corresponding to the diminution in the size of hats, shown in the two lower lines of the table, and if this diminution were to continue at the same rate until the year 1968, the English Nation would then have heads smaller than the average Andaman Islander, and they would soon be reduced to the condition of microcephalic idiots. Fortunately for the coming generation we need not anticipate such a change, and we may account for the difference in the figures by variations in circumstance, apart from diminution in size of head—*e.g.*, a difference in the mode of wearing the hat, and in the fact, as evidenced by photographs, that it is customary now to have the hair much more closely cropped than was the fashion in 1868. On considering the more recent statistics relating to measurements of the head and skull, it soon became evident that in order to obtain more definite results than hitherto, it would be necessary to draw my figures from a few well-defined classes of individuals who were living under approximately the same conditions; to keep these classes separate; and, in comparing the measurements of the classes with one another, and of the individuals composing each class, to contrast the extremes with one another, rather than to compare either extreme with a general mean; further, that the actual measurements should be recorded in the tables, or the number of measurements falling between certain figures lying close together (*e.g.*, the number in each class having heads measuring in height from 130-134 mm. and from 135-139 mm., etc.), rather than

counting the number falling above or below a certain general average.

One of my chief objects in this investigation has been to ascertain for myself whether, or not, there is a distinct increase in the size of the head and brain commensurate with an increase in the standard of mental ability; and conversely, whether there is or is not a decrease in size of head and brain correlated with a decline in intellectual power. The question involves the consideration of many others, and in dealing with it a number of circumstances have to be taken into account—*e.g.*, if it be granted that an increase in the size of head is associated with an increase in the standard of mental ability, is this increase in the size of the head simply proportional to, and correlated with, an increase of stature and body-weight, the result of the more favoured conditions under which a higher and more intellectual class of society is living? or are the gold medallists and prize-winners in a school or college a few years older than the others? and is the greater size of head in the former due to the natural enlargement of the head accompanying growth? also to what extent is the question complicated by the mixture of different types of individuals? further, does the emotional side of a person's organization, or the degree of muscular development, have any influence on the size and shape of the head, and if so, is the development of either or both of these in a high degree opposed to a high standard of mental ability, or may the three conditions all coexist in a highly developed state and be associated with an unusually large brain and head? Some of these questions have been very ably dealt with already by others, and may be considered to be more or less definitely answered, while others remain questions still. In certain cases the collateral conditions have not only been demonstrated to exist and to exert an influence on the size and shape of the head, but the degree of the influence has been quantitatively estimated, and the amount may be added or deducted from the general results of the investigation. The majority of these conditions, however, remain, and will continue to remain, quite unmeasurable; and their influence, which may be considered to account for a certain number of exceptional cases, must be counterbalanced by measuring a sufficiently large number of individuals, so that

their chance effect upon any one class or subdivision may be
reduced to a minimum.

The kind of influence that collateral conditions may have
upon the question which is the subject of this paper, may be
illustrated in the following manner. Let us suppose that the

Table II
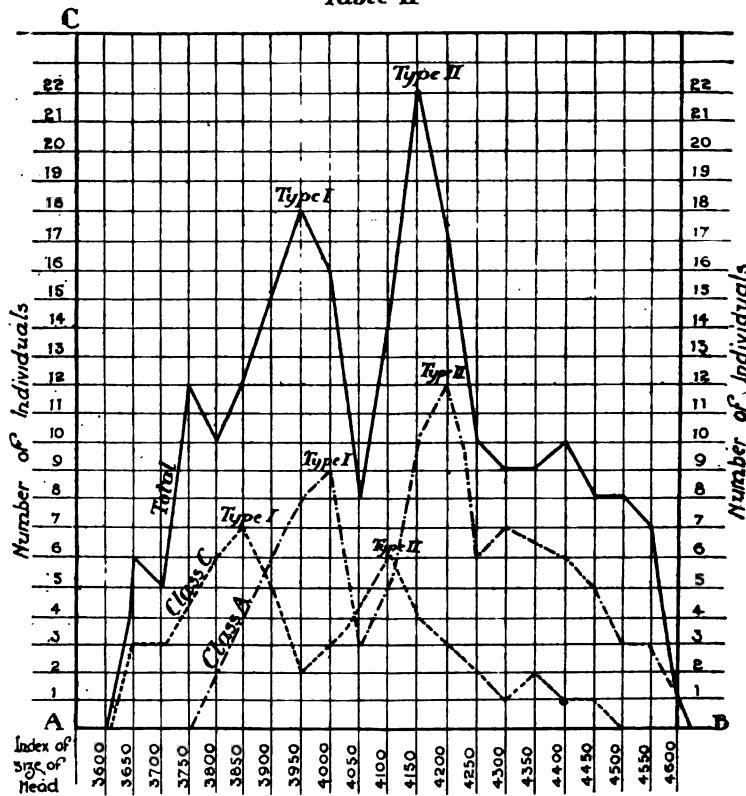
total number of individuals measured belong to two types, one
characterized by having a small head which we will call Type
I., the other by a large head which we may speak of as Type
II. If we draw out a ' frequency polygon ' (see Table II.) showing
the number of individuals having heads corresponding to
successive degrees of size, the figures denoting which are placed
along the abscissa A.B., the polygon will probably have two

main peaks, the apices of which will, by their position, indicate the size of head most frequently met with in the corresponding type; it will be seen that the apex of the peak corresponding to Type I. is opposite the figure 3950, and that of Type II. opposite 4150, while there is a marked drop between them at 4050.

Let us further suppose that in each type there are individuals with a high degree of mental ability, and having heads relatively larger than those with a low degree of ability and belonging to the same type, and let us call the former Class A, and the latter Class C, and let us leave out of consideration altogether the individuals of average intelligence, who would fall into an intermediate Class B, and let us map out the curve for each of these two classes within the main curve corresponding to the total number.   Each class will be seen to have two type peaks, which lie within the corresponding peaks of the main curve; but the peaks of Class A will be a little to the right of the corresponding peaks of Class C, and will thus indicate that in each type Class A have generally larger heads than those of Class C, although the individuals composing Class A and belonging to Type I. will have smaller heads than those of Class C belonging to Type II.   Moreover, if the average size of head of Class A in both types taken together be compared with the corresponding total average in Class C, it will be found to exceed the latter.

The apparent exceptions, therefore, to the rule that *individuals with great mental power have generally larger heads than those with small*, are easily accounted for by supposing that these exceptions belong to a type or race of men characterized by the smallness of their heads; and it will be seen also that the total averages of each class will, provided the number of individuals be sufficiently large, only be very slightly affected by the difference in types.

My figures do actually show a drop corresponding in position and extent to that represented in the main curve of the diagram, but the line extends in an irregular manner for a considerable distance on each side beyond the limits of the diagram, and I wish it to be clearly understood that I have inserted the chart merely for the purpose of illustrating a

principle, and that it does not represent an accurate record of my measurements.

These measurements I have grouped together in a series of tables, most of which I have constructed on the following simple plan. The individuals composing each group have been divided into three classes, according to the degree of their mental ability : these classes I have called A, B, and C. Class A comprises the gold medallists, scholarship, and prizemen, individuals with keen intellect, sound judgment, and versatile in talent; Class B, those of average intelligence ; and Class C, individuals with poor memory, slow intelligence, with little or no power of reasoning, and conspicuously wanting in initiative or originality. The minimum, average, and maximum measurements of each class have been found and arranged in three horizontal lines, Class A being above, Class B in the middle, and Class C below; in this way three vertical columns are formed showing the minimum, average, and maximum measurements of each of the three classes (see Table III.).

The individuals which I have been able to classify in this way belong to two main groups :—(a) the students and medical staff of the Middlesex Hospital, of whom I have the measurements of rather more than 200, and (b) the boys of St Katherine's School, Regent's Park, numbering 42. In each group the individuals comprised in Class B are the most numerous, those in Class C the least numerous, while Class A is intermediate in number.

Besides these two groups I have the measurements of 50 male and 100 female subjects (over 50 years of age), inmates of the St Pancras Workhouse; and I am obtaining the measurements of 50 male and 50 female subjects from the post-mortem room of the Middlesex Hospital, in which the brain-weight is recorded in addition to the outside measurements. The latter number, however, is not yet complete, and I only mention them here, because I have already made use of them in finding a provisional ratio between the weight of the brain and the outside measurements of the head.

The data which I have selected as the most important, and have employed in constructing the following tables, are the

sex, age, weight, and stature of each individual, with the following measurements of the head :—

l, the length of the head, from the glabella to the occipital point.

b, the maximum transverse diameter of the head above the level of the zygomatic arches.

h, the height of the cranium, as indicated by the vertical distance from the biauricular line to the bregma.

c, the horizontal circumference, taken in a plane passing in front through a point just above the glabella and behind through the occipital point.

I have also obtained tracings of the horizontal contour of the head, and a full and profile photograph of the majority of individuals composing the Middlesex Hospital group, besides other data such as the colour of the hair and eyes, the degree of muscular development, the circumference of the chest, the longitudinal and transverse arcs of the head, the nationality and birth-place, and a few notes indicating the personal status and hereditary conditions of each individual.

The longitudinal and transverse diameters have been taken with Mr J. Gray's callipers, a full account of which will be found in the *Journal of the Anthropological Institute*, vol. xxxi., 1901, p. 111. These have the advantage of acting automatically, and thus giving the same measurements when used by different individuals. The height of the head and the horizontal contour have been recorded by the instruments figured and described in the Report of the *Proceedings of the Anatomical Society*, November 1901.

My first table, III., indicates the minimum, average, and maximum sizes of head among the students of the Middlesex Hospital, including a few qualified practitioners who have attended senior classes in that institution.

The figures, which give an indication of the relative sizes of the heads measured, have been obtained by multiplying together the three principal diameters of the head, l, b, h, expressed in millimetres thus—

$$l\,(196) \times b\,(156) \times h\,(138) = 4219'488.$$

The first four figures of this number, 4219, represent the number of cubic centimetres which would be contained in a rectangular block having diameters corresponding to the above diameters of the head, and I shall refer to the number subsequently as the *Index of Size* of the head; and although it is not quite directly proportional to the actual size of the head and its contents, owing to differences in shape and in the thickness of the skull and its coverings, I have found it sufficiently so for practical purposes.[1]

TABLE III.—*Students of the Middlesex Hospital.*
Indices of Size.

				Min.		Aver.		Max.
Class A,	.	.	.	3849	...	4320	...	5100
Class B,	.	.	.	3523	...	4015	...	4808
Class C,	.	.	.	3486	...	3747	...	3990

This table shows a progressive diminution in the size of the head from Class A to Class C, and it also shows that the man with the largest head belongs to Class A, and the one with the smallest to Class C. Moreover, the average index of size of Class B (4015) is considerably above the general average of the uneducated classes, and indicates an approximate brain-weight of 1439 grammes.

[1] (1) The last three figures of the total product form a fraction of a cubic centimetre, which will on the average amount to $\frac{1}{2}$ c.cm., and which I have thought sufficiently small to leave out of consideration; it is important, however, to use the greatest care in taking the measurements, and, if the measurement of any or all of the diameters of the head falls a little beyond or short of the millimetre mark on the scale, to record the fraction, for if we compare the product l, b, h, quoted above ($196 \times 156 \times 138$) $= 4219'488$, with the product of the same diameters each increased by 0·5 mm. ($196·5 \times 156·5 \times 138·5$) $= 4259'186$, it will be seen that there is the very considerable difference in the 'index of size' of 40 c.cm. ($4259 - 4219 = 40$).

(2) In dealing with large numbers it is not necessary, in order to find the average size of the head or other 'organ,' to work out the product of the diameters (l, b, h) in each case and then find the mean of these products, for, as has been shown by Dr Alice Lee and Professor Karl Pearson in the case of skulls belonging to various races, the mean of each of the three diameters (l, b, h) for the group under consideration may be found, and these three means multiplied together will give a result differing by less than 1 per cent. from the mean of the products, to find which would entail a very much greater expenditure of time and labour.

(Dr Alice Lee and Professor Karl Pearson, *Phil. Trans. Roy. Soc. London,* Series A., vol. 196, p. 249 (13)).

The next table, IV., shows the indices of size of the boys of St Katherine's School, Regent's Park, the degree of mental ability of whom was estimated by the schoolmaster engaged in teaching them, and who was intimately acquainted with the character and status of each. The age of the boys ranges from 7–14 years, and the average age and height of the three classes is almost equal. .

TABLE IV.—*Boys of St Katherine's School.*
Indices of Size of Head.

	Min.		Aver.		Max.
Class A,	2850	...	3419	...	3998
Class B,	2951	...	3218	...	3657
Class C,	2937	...	3151	...	3962

It will be noted that here also there is a progressive diminution in the average size from Class A to Class B, and that the boy with the largest head belongs to Class A, the boy with the smallest head, however, is also in Class A, and the maximum of Class C is very little below that of Class A. ·

Table V. gives the average indices of size for different groups, including the Anatomists who were measured in the Anthropometrical Laboratory of Trinity College, Dublin, at the meeting of the Anatomical Society in 1898, and for the Report on the measurements of whom I am indebted to Professor D. J. Cunningham and Dr C. R. Brown.

TABLE V.—*Average Indices of Size of Different Groups.*

Middlesex Hospital Medical Staff,	.	.	4317
Anatomists at Trinity College,	.	.	4161
Middlesex Hospital Students,	..	..	4015
Men in St Pancras Workhouse,	.	.	3933
Women in St Pancras Workhouse,	.	.	3482

The following six tables show the length, breadth, and height of the head, expressed in millimetres, of the three classes in the Middlesex Hospital and St Katherine's School groups; and it will be observed, on comparing the averages, that Class A is in all cases the highest, and that there is a progressive diminution from A to C, except in the column showing the mean height of head in the St Katherine's School group, where Class C exceeds Class B by one millimetre. The decimal points have, for the sake of simplicity, been omitted in all cases. ·

TABLE VI.—*Middlesex Hospital.*
Length of Head.

	Min.		Aver.		Max.
Class A, . . .	189	...	199	...	209
Class B, . . .	183	...	196	...	210
Class C, . . .	188	...	193	...	201

TABLE VII.--*St Katherine's School.*
Length of Head.

	Min.		Aver.		Max.
Class A, . . .	175	...	187	...	197
Class B, . . .	170	...	183	...	194
Class C, . . .	173	...	179	...	188

TABLE VIII.—*Middlesex Hospital.*
Breadth of Head.

	Min.		Aver.		Max.
Class A, . . .	141	...	154	...	168
Class B, . . .	138	...	153	...	168
Class C, . . .	140	...	148	...	155

TABLE IX.—*St Katherine's School.*
Breadth of Head.

	Min.		Aver.		Max.
Class A, . . .	130	...	144	...	156
Class B, . . .	135	...	143	...	152
Class C, . . .	134	...	142	...	153

TABLE X.—*Middlesex Hospital.*
Height of Head.

	Min.		Aver.		Max.
Class A, . . .	130	...	140	...	155
Class B, . . .	127	...	138	...	148
Class C, . . .	121	...	131	...	138

TABLE XI.—*St Kathcrine's School.*
Height of Head.

	Min.		Aver.		Max.
Class A, . . .	115	...	127	...	143
Class B, . . .	118	...	123	...	130
Class C, . . .	117	...	124	...	133

The next table shows the range and frequency of different vertical diameters of Classes A, B, and C in the Middlesex Hospital group, arranged in successive degrees of height; it

will be seen that Class C is entirely confined to the four lowest stages, Class A to the five upper, while Class B occupies the five middle.

TABLE XII.—*Middlesex Hospital.*

Height in Millimetres.			Percentage Frequency.			
			Class C.		Class B.	Class A.
150–155	...	...	...	...	...	3
145–149	...	...	...	...	11	13
140–144	...	...	...	...	15	40
135–139	...	27	...	43	...	33
130–134	...	27	...	22	...	9
125–129	...	36	...	6	...	...
120–124	...	9	...	...	...	...

The decimal points have, for the sake of simplicity, been omitted.

The next table gives the average horizontal circumference of the head in millimetres for the three Classes A, B, and C in the Middlesex Hospital and St Katherine's School groups.

TABLE XIII.—*Average Circumference of Head.*

Middlesex Hospital.			St Katherine's School.		
Class A.	Class B.	Class C.	Class A.	Class B.	Class C.
572	562	555	541	526	515

It will be observed that there is a progressive diminution from A to C in both groups.

The two succeeding tables show the proportion that the calculated brain-weight bears to the body-weight; the fraction indicating this is obtained by dividing the calculated brain-weight by the body-weight, and I shall refer to it as the 'encephalo-somatic index.'[1]

TABLE XIV.—*Encephalo-somatic Index.*

	Middlesex Hospital.			St Katherine's School.		
	Min.	Aver.	Max.	Min.	Aver.	Max.
Class A,	0·0182	0·0218	0·0288	0·0356	0·0465	0·0640
Class B,	0·0159	0·0203	0·0268	0·0311	0·0409	0·0554
Class C,	0·0191	0·0200	0·0218	0·0350	0·0408	0·0521

[1] This ratio may also be expressed in the following manner :—

$$\frac{1000 \times \text{Brain-weight}}{\text{Body-weight}} = \text{Encephalo-somatic Index},$$

and the fraction thus got rid of. The meaning of the figures is, however, more self-evident in the form stated above, and I have thought it best for this reason to retain the fraction.

The rise in the average index in passing from Class C to Class A is seen to be very considerable, and especially so in the case of the boys.

The three following tables show the cephalic indices of the Middlesex Hospital and St Katherine's School groups, and a combination of these, which shows a slight tendency towards dolichocephaly in Class A when compared with Classes B and C. The higher cephalic indices of these two classes are obviously not due to the individuals composing them having actually broader heads than those of Class A, as will be seen by comparing these tables with the foregoing; but it is due to the comparatively greater length of head in the individuals of Class A.

TABLE XV.—*Cephalic Index.*
Middlesex Hospital.

	Min.		Aver.		Max.
Class A, . . .	70·6	...	77·4	...	84·3
Class B, . . .	71·0	...	78·4	...	85·8
Class C, . . .	70·3	... ·	76·6	...	81·3

TABLE XVI.—*Cephalic Index.*
St Katherine's School.

	Min.		Aver.		Max.
Class A, . . .	68·4	...	77·0	...	81·4
Class B, . . .	72·1	...	78·1	...	81·5
Class C, . . .	75·1	...	79·3	...	84·3

TABLE XVII.—*Cephalic Index.*
Middlesex Hospital and St Katherine's School.

	Min.		Aver.		Max.
Class A, . . .	69·5	...	77·2	...	82·8
Class B, . . .	71·5	...	78·2	...	83·6
Class C, . . .	72·7	...	77·9	...	82·8

Tables XVIII. and XIX. show the proportion that the height of the head (from the biauricular line to the vertex) bears to its horizontal circumference, the latter being expressed as 100. This ratio I have termed the 'auriculo-bregmatic index,' and use it in place of the 'length-height index,' because the circumference being proportional to both length and breadth, gives a better indication of the general size of the head, taken in the horizontal plane, than the length alone.

$$\frac{100 \times \text{Height}}{\text{Circumference}} = \text{Auriculo-bregmatic Index.}$$

On looking at the column containing the average indices in the Middlesex Hospital group, it will be noticed that there is a progressive increase from C to A, showing that there is not only an absolute increase in the height of the head with an increase in mental ability, but also an increase relative to the other dimensions of the head. This is not the case, however, with the boys of St Katherine's School, in which, although the highest index occurs in Class A, and the lowest in Class C, the average for Class C is above that of both A and B.

TABLE XVIII.—*Auriculo-bregmatic Index.*
Middlesex Hospital.

	Min.		Aver.		Max.
Class A, . . .	21·7	...	**25·0**	...	**26·8**
Class B, . . .	22·3	...	24·2	...	**27·5**
Class C, . . .	21·2	...	23·6	...	24·9

TABLE XIX.—*Auriculo-bregmatic Index.*
St Katherine's School.

	Min.		Aver.		Max.
Class A, . . .	21·9	...	23·7	...	**27·7**
Class B, . . .	22·6	...	23·4	...	24·7
Class C, . . .	20·9	...	**24·2**	...	25·3

The last table, XX., shows the excess in millimetres of Class A over Class C, which occurs in the three average diameters, and in the two groups, viz., the Middlesex Hospital group as representing adult measurements, and the St Katherine's School the measurements in boys.

TABLE XX.

	Average Measurements.				Excess of
	Class A.		Class C.		A over C.
Middlesex Hospital,	Length, 199	...	193	...	6 mm.
St Katherine's School,	Breadth, 187	...	179	...	8 mm.
Middlesex Hospital,	Length, 154	...	148	...	6 mm.
St Katherine's School,	Breadth, 144	...	142	...	2 mm.
Middlesex Hospital,	Length, 140	...	131	...	9 mm.
St Katherine's School,	Breadth, 127	...	124	...	3 mm.

The tables thus show a distinct correlation between large

size of head and a high degree of mental ability, this correlation being both absolute and relative to the general size and weight of the body. In adults the increase in size of head appears chiefly in the vertical diameter, which should always be included in making any estimate of the size of the head; in the boys the increase is chiefly in the longitudinal diameter, as has been demonstrated also by Dr Alfred Binet in an article entitled "Études Préliminaires de Céphalométrie sur 59 Enfants d'Intelligence Inégale choisis dans les Écoles Primaires de Paris," contained in *L'Année Psychologique*, Septième Année, p. 369.

There are many other questions bearing upon this subject which will well repay a farther investigation; such as the relationship of nationality and heredity to the size and shape of the head, and the connection of these with varying degrees of mental ability; and in concluding this small contribution to a large subject, I must express the hope, that I entertain, of adding to these statistics with the view of confirming, or otherwise, the results which I have already obtained, and of gaining some fresh lights upon problems which are for the present still obscure. I have also to thank the Rev. Mr J. B. Peile, Master of St Katherine's School, for his kind permission to measure the boys, and the Managing Committee of the St Pancras Workhouse, and others who have helped me in this investigation, and more especially Mr Freke Field, who has taken with great exactitude the majority of the measurements, and borne a large share in carrying out the statistical work.

THE FORM-RELATIONS OF THE DILATED CEREBRAL VENTRICLES IN CHRONIC BRAIN ATROPHY.

By J. O. WAKELIN BARRATT, M.D. Lond., F.R.C.S. Eng.

THE present paper is a continuation of investigations, already published, on the form and relations of the normal cerebral ventricles,[1] and on the form of the dilated ventricles met with in chronic brain atrophy occurring in the insane.[2] The relation of the form of the dilated ventricles to the form of the brain as a whole, and to some of its more important constituents as studied in four cases, has now to be described.

Method.

Of the four brains whose ventricular cerebral cavity was examined, the first (No. 1 in the table, p. 353) was removed at the autopsy and placed in a saturated solution of potassium bichromate, hardening being completed at the end of eight months. In this fluid the brain at first floated, so that the risk of changing the form of the brain during hardening was inconsiderable. The remaining three brains were hardened *in situ* by the injection of 10% formol solution into the cerebral arteries prior to opening the skull. In all these cases hardening of the cerebellum, pons, medulla, and base of the cerebrum was complete, but the whole of the vertex had not been reached by the injection, so that it was necessary to continue the hardening process after removal; but the brain was found to be so far hardened on removal, that it retained its shape without change. The removal of the injected brain was readily effected by sawing off the skull-cap close to the base of the cranium.

Of these two modes of hardening, the first does not preserve the form of the brain so faithfully as the latter, since the support of fluid during hardening is not so perfect as that of the skull. After the injection of formol, no doubt can be entertained of the correctness of any slight obliquity or

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[1] *Journ. of Anat. and Physiol.*, 1902, vol. xxxvi. pp. 106–126.

[2] *Ibid.*, 1903, vol. xxxvii. pp. 150–167.

asymmetry which is present.   The injection of formol, however,
causes some swelling of the brain substance, and thus tends to
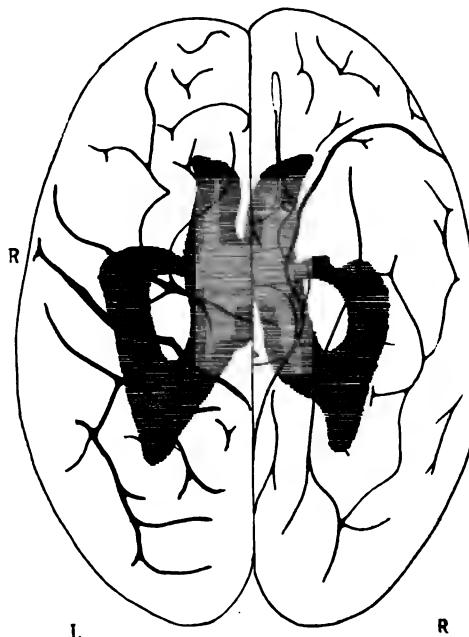
FIG. 1B.—Plan of the brain of Case 1.   On the left is the upper surface of the
  left hemisphere seen from above ; on the right is lower surface of the right
  hemisphere also viewed from above.   The plan of the cerebral ventricular
  cavity is inserted *in situ*, so that its relation to the cerebrum can be observed.
  On the left side the fissure of Rolando, R, together with the ascending
  frontal and intra-parietal fissures, are shown ; on the right side the anterior
  limit of the right temporal lobe is seen, together with the optic chiasma,
  the tuber cinereum, and the mesencephalon cut across at its junction with
  the pons Varolii.   This plan is made with reference to the horizontal plane
  shown in fig. 1A.   Figs. 2B, 3B, and 4B are constructed in the same way.
    There is asymmetry of the lateral ventricles in respect of each other,
  while the bodies of the lateral ventricles, together with the third ventricle,
  are displaced to the left.   The tips of the anterior cornua do not reach as
  far forwards as the tips of the temporal lobes.   The anterior cornua are
  not disproportionately large as compared with the rest of the lateral
  ventricles.

R, right ; L, left.

This and the succeeding figures are one-half the natural size.

diminish the ventricular cavity, for which reason it is not
desirable to use a large quantity of injecting fluid ; if the brain

is sufficiently hardened to retain its form, the completion of the hardening may best be carried out after removal.

The hardening being completed, the plan of studying the form-relations of the cerebral ventricles was similar to that adopted in the previous work. A horizontal plane (*Cp.* figs. 1B, 2B, 3B, 4B) was marked out on the surface of the brain, and then a series of equidistant frontal planes. Plans of the
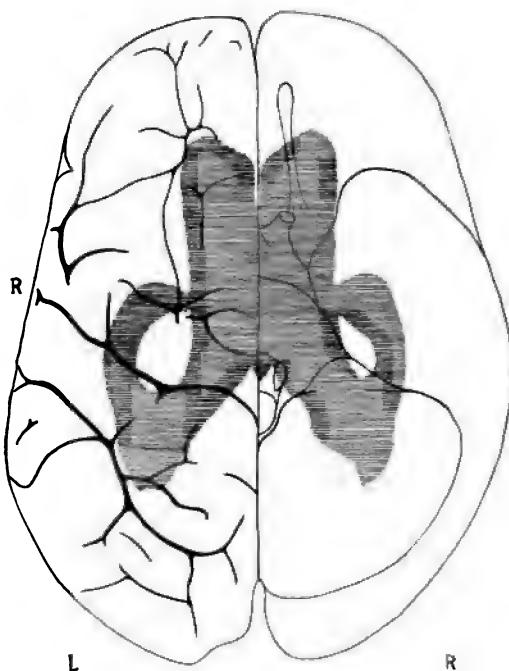
FIG. 2B.—Plan of the brain of Case 2, seen from above as in fig. 1B. The same asymmetry of the lateral ventricle is exhibited as in the preceding case.

brain, seen from above, below, and the sides, were then drawn accurately to scale. The frontal sections, already marked out, were then made and sketched. By means of the latter the ventricles of the cerebrum were reconstructed, and a tracing of the same inserted in each of the plans previously made.

Some practice is required before a sufficient degree of accuracy is acquired to permit of an exact representation of the ventricular cavity. In particular it is necessary to avoid

perspective representations, and to construct only plans and side elevations. As some difference of opinion may exist as to what should represent a horizontal plane in the case of the brain, the latter is represented in the sketches by the horizontal line in figs. 1 to 4, A, and the frontal planes referred to above were made at right angles to this plane.

Finally, the slices of brain were in each case put together
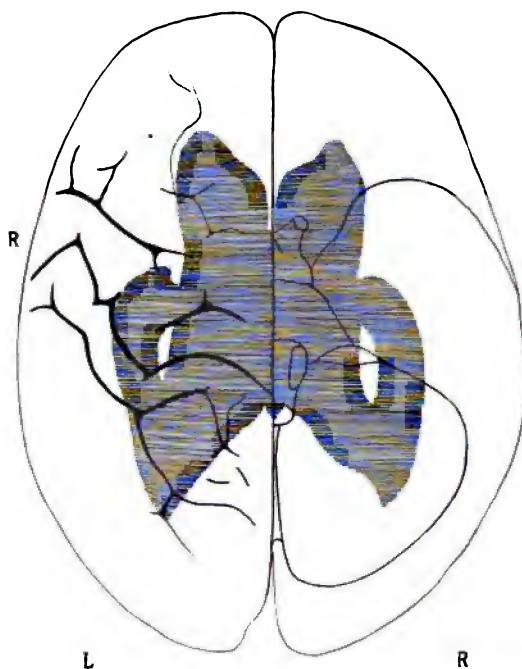
FIG. 3B.—Plan of the brain of Case 3, seen from above. As before, some asymmetry of the lateral ventricles is present, chiefly in the posterior cornua.

again, and a plaster of Paris cast of the cerebral ventricles made. It was not possible in this procedure to secure perfectly accurate apposition, nor, indeed, altogether to avoid distortion, so that the cast had not the same value as the reconstructed ventricular cavity. Nevertheless it afforded a useful criterion of the truthfulness of the reconstructed cavity, formed a check upon accidental inaccuracies, and furnished much valuable information in respect of details of form, while at the same time permitting

thicker slices of the brain (and therefore fewer in number) to
be made than would have been otherwise possible.   A practical
detail may here be referred to.   In dissecting out the plaster
cast, fracture always occurs at the junction of the third and
one of the lateral ventricles.   As soon, therefore, as the interval
corresponding to the septum lucidum is reached, this should
be filled up with plaster of Paris before any displacement of
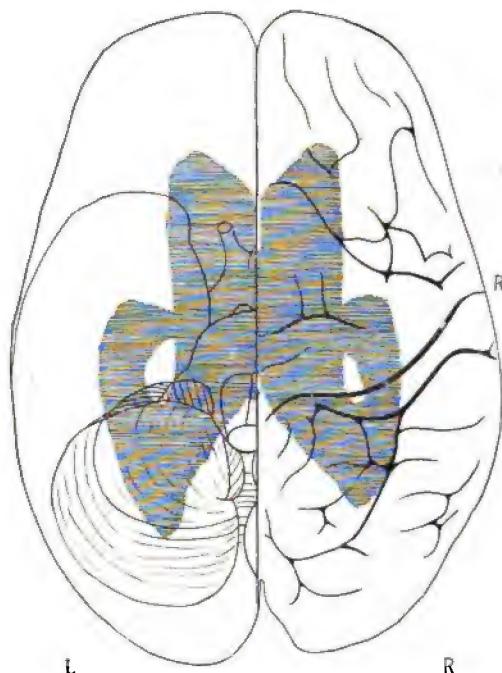
FIG. 4B.—Plan of the brain of Case 4, seen from above.   Asymmetry is present
both in the form of the ventricles and in that of the brain.   The cerebellum
and medulla appear displaced to the left of the middle line.

the fragments has occurred.   In this way a cast is obtained
which is less fragile than would be the case if the lateral
ventricles were connected only to the third ventricle.

Form-relation.

The cerebral ventricular cavity may naturally be expected to
vary in relation to the general form of the brain, and more par-

ticularly according as the head is broad or narrow. Thus, if the
brain of a dolichocephalic individual is compressed in its antero-
posterior diameter so as to change it towards the brachycephalic
type, the basi-bregmatic height remaining all the time unchanged,
the ventricular cavity would tend to become broader from side to
side; while if, on the contrary, the altitudinal index were simi-
larly increased, the cerebral lateral ventricles would tend to be-
come correspondingly arched from before backwards. The small
number of cases examined did not permit of any generalisation
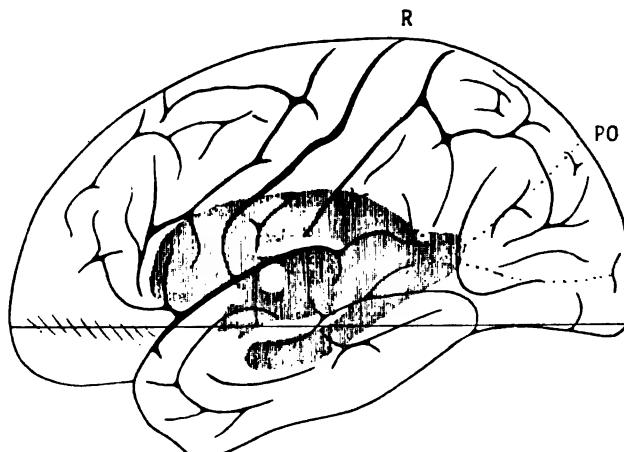
FIG. 1A.—Side elevation of the brain of Case 1. The fissure of Rolando, R,
   together with the ascending frontal, the intra-parietal, parieto-occipital, PO,
   and the calcarine fissures are shown, and an elevation of the third and right
   lateral ventricles inserted *in situ*. Note that the brain does not reach
   vertically so high as the succeeding brains, and the lateral ventricle is
   correspondingly flattened from above.

being made, and the divergences in type of the cases examined
were not considerable, the cephalic indices varying between 73·7
and 78·8, and the altitudinal indices between 68·3 and 79·0
(see table); but, as the sketches indicate, a conformity in the
relation of ventricular to cerebral form was found to exist in
the brains examined. Thus, in brains 2 and 4 (latitudinal indices,
73·7 and 75·0) the distance between the inferior cornua relatively
to the bodies of the lateral ventricles was greater than in brains
1 and 3 (latitudinal indices, 76·0 and 78·8); and again, the first
three brains, which had nearly the same altitudinal index (68·5,

68·3, and 70 respectively), were more flattened, as seen in side elevation, than brain 4 (altitudinal index, 79). To satisfactorily establish such a relation, however, a large number of healthy

Table giving Particulars of the Brains Examined.

No.	Mental State.	Condition of Brain.	Weight of Brain.	Capacity of Cerebral Ventricular Cavity.	Latitudinal Index.	Altitudinal Index.	Brain : Cerebral Ventricles.
1	Epileptic dementia	Wasted	1225 g.	37·5 c.c.	76·0	68·5	100 : 3·1
2	Senile dementia	Much wasted	1160 ,,	47 ,,	73·7	68·3	100 : 4·3
3	General paralysis	Wasted	1300 ,,	97 ,,	78·8	70·0	100 : 7·5
4	General paralysis	Wasted	1220 ,,	110 ,,	75·0	79·0	100 : 9·8

brains, presenting a greater variation of form than the few we have had the opportunity of studying, require to be examined.

There is another factor, which determines the general form of
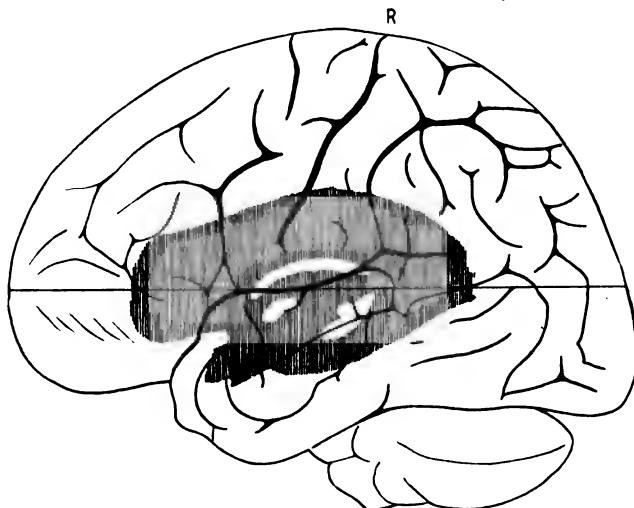
Fig. 2A.—Side elevation of the brain of Case 2. The brain is more arched above than in the preceding case, and the ventricular dilatation is much greater. The anterior cornu is relatively more enlarged than the rest of the lateral ventricle.

the dilated cerebral cavity, and that is the manner in which the brain wastes.   If the brain wasting associated with ventricular dilatation were equally distributed, the increased size of the ventricular cavity would in all cases present the same divergence from the original type, increasing *pari passu* with the degree of wasting.   As a matter of fact, the wasting is unequal, and this
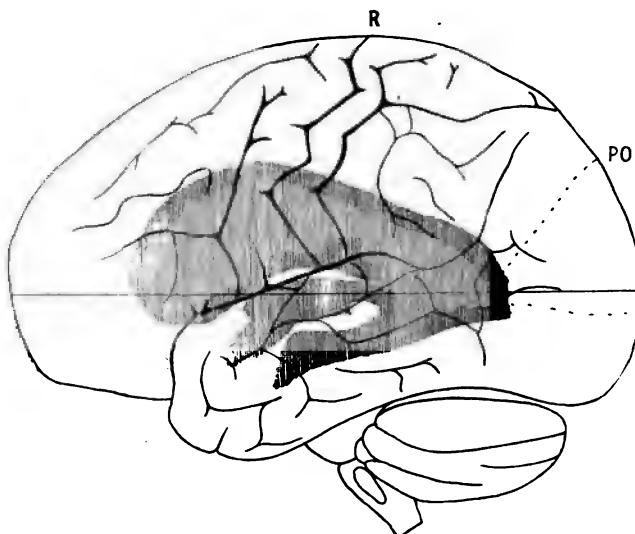
FIG. 3A.—Side elevation of the brain of Case 3.   The vertex of this brain forms a well-marked arch, and the dilatation of the ventricles, which is striking, affects the anterior cornua and the bodies much more than the rest of the lateral ventricles   The width from above downwards of the third ventricle is less than in the preceding figures.   The middle commissure is absent. The dilatation of the lateral ventricles is far greater than that of the third ventricle.   The fissure of Rolando, R, is less simple than in the other brains represented.

disturbs the relation between the form of the dilated and that of the original cavity, by causing disproportionate local increase in size, which is the more marked the greater the brain atrophy. Thus, in all the cases examined, the wasting had affected the frontal and parietal lobes more than the rest of the brain mantle, the difference being especially noticeable in the general paralytic brains 3 and 4, and correspondingly influencing, as a glance at the figures shows, the shape of the anterior cornua and bodies of the lateral ventricles, which had undergone a far

greater relative increase than the rest of the ventricular cavity. Here again it may be observed that in brain atrophy of the insane the dilatation of the lateral ventricles, which, in its way, forms the negative of the corresponding wasting of the brain mantle, is, as is well known, very considerable relatively to that of the third ventricle, embedded in the thalamencephalon, which undergoes little alteration in size.

Other points in connection with the general relation between
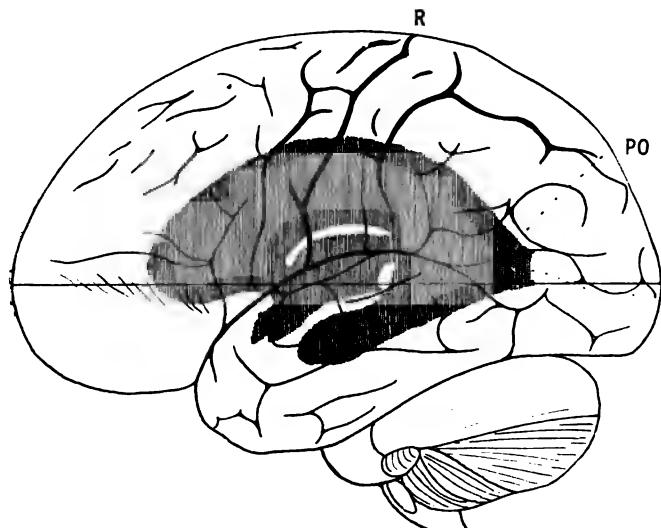
FIG. 4A.—Side elevation of the brain of Case 4.   Considerable dilatation of the cerebral ventricles exists, and the lateral ventricles are much more arched than in any of the preceding illustrations.   The dilatation affects principally the anterior cornua and bodies of the lateral ventricles.

ventricular form and cerebral form naturally suggest themselves as the sketches are studied, but it is perhaps better, as the number of cases before us is so small, to defer further speculation until a large series of brains has been investigated, and to remain for the present content with merely putting on record, as far as possible graphically, the conditions present in the cases now under consideration.

In passing to study details of form-relation, we naturally turn first to the fissures of the brain as presumably standing in a constant position in respect of the ventricular cavity.   But at the outset it becomes clear that the smaller fissures are too

variable to be of much value in forming landmarks in respect
of ventricular dilatation, and the same difficulty also arises in a
lesser degree in respect of the main fissures—namely, the fissures
of Sylvius and Rolando and the parieto-occipital sulci. Sherring-
ton and Grünbaum,[1] in the case of the motor area, have shown
that the fissures do not correspond to motor centres, and there-
fore afford but limited assistance in localisation—all this being
in striking contrast to the far greater constancy and symmetry
of bilateral situation of these centres. The same is presumably
true of the relation in respect of function of the sulci of the
brain mantle elsewhere. And as variations in the manner of
folding of the brain mantle may be supposed to influence within
certain limits the form of the normal ventricular cavity, so the
same circumstance may also cause variations in the trace of the
fissures (of Rolando, parieto-occipital, etc.) in respect of the
ventricular cavity as exhibited in a plan or side elevation of the
brain. Moreover, the further difficulty arises that when a fissure—
for example, the fissure of Rolando—is mentioned, merely the
base of the fissure as it appears on the surface is usually referred
to, and the sulcus in its depth is left out of consideration. As the
former is not necessarily a faithful index of the latter, it is
obvious that the base of the sulcus is not of great value in
respect of the determination of the form-relation of the ven-
tricular cavity. Nor does it seem possible to obtain much
greater accuracy by attempting to simplify the trace of the
fissure of Rolando by representing it as a single line whose
direction may be taken to indicate the mean position of the
sulcus in its depth, for such a line could hardly be determined
with sufficient accuracy to be of value when the fissure of
Rolando is complicated in character as in fig. 3B.

Bearing in mind that the fissures of the brain are within
certain limits variable, and that their relationship therefore to
the cerebral ventricles is not one of precision, we may now
briefly refer to this relationship so far as it concerns, in the
brains studied, the main fissures—namely, those of Rolando and
Sylvius (posterior limb) and the internal parieto-occipital sulcus
—the position of which is exhibited in the figures.

[1] *Brit. Med. Jour.*, 1901, ii. p. 1858. *Cp.* also Schäfer, *Festschrift zu Karl
Ludwig*, 1887, Leipzig.

In its general direction in side elevation the fissure of Rolando, as a glance at the figures will show, was found to run from or near the junction of the third and lateral ventricles upwards and backwards to a point a little behind the middle of the vertex, only the lower half to third lying over the middle of the body of the lateral ventricle; while in the plan this fissure lay more posteriorly and nearer the middle line over the body at its junction with the posterior cornu, and also over the inferior cornu.

The posterior limb of the fissure of Sylvius in its middle third corresponds approximately to the upper border of the third ventricle, but the correspondence exhibited some variation, as the figures show.

The internal parieto-occipital and calcarine fissures come into relation with the posterior cornua, especially when these are prolonged some distance backwards into the occipital lobes. In the brains examined, however, the posterior cornua were short, and lay in side elevation opposite the junction of these two figures.

In addition to an acquaintance with the arrangement of the main sulci in regard to the ventricles, a knowledge of the position of the ventricular cavity in respect of the main outlines of the brain is of great assistance in enabling a mental picture of this cavity to be formed in a brain which is viewed from without. A few of these relations exhibited by the figures may be here referred to.

The anterior cornua reached approximately as far forwards as the tips of the temporal lobes when the dilatation was small (*cp.* fig. 1, A, B), and, as the dilatation increased, the anterior cornua came to lie in front of the tips of the temporal lobes (as in figs. 2 to 4, A, B). In the figures the anterior cornua are seen to reach to a distance from the tips of the frontal lobes, which amounts in each case respectively to 22%, 18%, 12%, and 20% of the antero-posterior diameter of the brain. Further data of the same kind may be determined, if desired, by the help of the figures which represent the actual distances [1] apart from the various structures exhibited in plan or elevation, in conjunction, if necessary, with the measurements given in the table.

The inferior cornua corresponded in side elevation very nearly to the middle third of the second temporal convolution,

[1] Reduced to one-half in reproduction.

or lay slightly below this portion of the gyrus. The anterior limit of the inferior cornu was represented in plan by the posterior border of the optic chiasma, or lay somewhat behind this level. The position of the inferior cornua, seen in plan, in respect of the temporal lobes, is better ascertained by reference to the figures than from a description in words.

The posterior cornua, as is well known, vary so widely in different brains as to their form and the extent to which they pass backwards into the occipital lobes, that each individual case requires a separate description, and no generalisation seems possible. In the four cases examined they were very short.

The anterior limit of the junction of the body and inferior horn of the lateral ventricle lay in or slightly behind a frontal vertical plane passing through decussation of the anterior pyramids in the medulla, and passing above, through, or a little in front of the superior extremities of the Rolandic fissures. In plan the inner border of the body was found to lie close to the middle line or even to pass a little distance to the distal side of the middle line, while the outer border lay approximately midway between the mesial plane and the outer margin of the brain; but its curvature varied in the different brains, and the extent to which it passed outwards was greatest in Case 4, in which the degree of atrophy was also most marked.

As regards the third ventricle, in plan the tip of the preoptic recess corresponds to the anterior border of the optic commissure. The supra-pineal recess was found to be so variable that its position required separate description in each individual case. The upper end of the aqueduct of Sylvius, however, was more constant in position. It lay in the brains studied nearly vertically above the decussation of the anterior pyramids of the medulla oblongata. In brains 3 and 4 no middle commissure was present.

The foregoing observations, which were undertaken in the course of an investigation of chronic brain atrophy in the insane, are of necessity fragmentary in character as they are also limited in number. It is hoped that the data herein contained may be of use as a record of the relative form of the dilated cerebral ventricles in respect of the atrophied brains in which they exist.

ABNORMALITIES IN THE SACRAL AND LUMBAR VERTEBRÆ OF THE SKELETONS OF AUSTRALIAN ABORIGINES. By Dr W. Ramsay Smith, *Adelaide, S.A.*

THE sacrum, No. 866, from a female aboriginal, consists of five pieces. The sacral canal is open posteriorly for its whole length, and passes to the left of the spinous process of the third, and to the right of the spinous process of the fourth and fifth vertebræ. It divides the spinous processes of the others.

On the left side, the alar portion of the first vertebra passes upwards and forms a synchondrosis with the enlarged costal
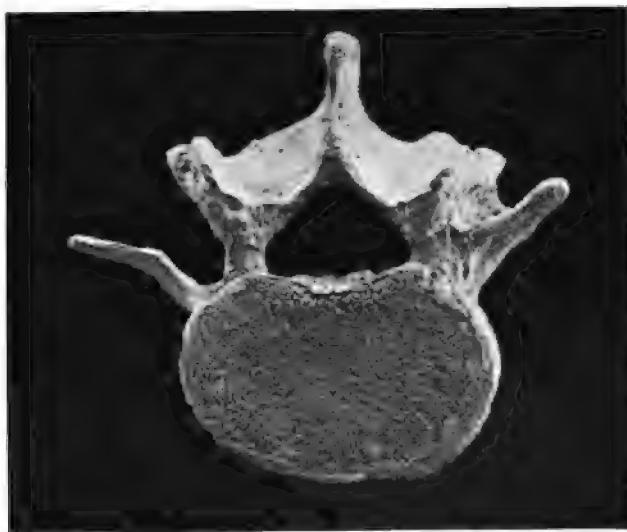
process of the fifth lumbar. This synchondrosis passes outwards, dividing the auricular surface into two portions—a sacral and a lumbar.

The fifth lumbar vertebra has its body thicker on the left than on the right side ; and its arch is incomplete posteriorly. It will be evident that this vertebra partakes of the characters of a sacral vertebra on its left side, and of a lumbar vertebra on its right.

The fourth lumbar vertebra presents an abnormality on its

right side; the transverse process springs from the side of the body in front of the pedicle, and with no connection either with it or the superior articular process (see figure).

The sacrum numbered 872 is composed of six normal pieces. The one numbered 873 is composed of the typical number, five. I have examined an aboriginal specimen with four.

A sacrum, No. 842, in which the body of the first vertebra was not ossified to that of the second : the spine is bifid, the inferior articular processes are free and not fused with the superior of the second, the right lateral mass is completely fused with that of the second, the left lateral mass is fused only at its tip.

These specimens are specially interesting as forming a graduated series in Australian aboriginals from four normal pieces, which is not uncommon, through four and a half, five, five and a half, to six normal pieces. They illustrate the transitional characters at the junction of the lumbar and sacral regions.

Recently, on examining a mounted skeleton belonging to Dr R. S. Rogers of Adelaide, I observed an abnormality which he had not noticed, and which he has permitted me to describe.

The skeleton was an imported one, made up, evidently, of the bones of white subjects, but of such a 'composite' character that one could not say with any degree of certainty what parts belonged to males, and what to females. The sacrum was of normal size, but the antero-posterior curve was much exaggerated.

The sacrum, which is fused into one bony mass with the coccyx, is formed of five sacral vertebræ.

On the left side, the first sacral vertebra has its alar portion only slightly developed : and this portion passes upwards and backwards to form a synchondrosis with the more truly alar border of the sacrum, which is formed by the second vertebra. In this instance the synchondrosis passes so much upwards, that the costal process of the first vertebra is cut off from articulating with the ilium.

The first vertebra has two distinct articulations with the second. The third has an abnormally large spinous process. The spinal canal is open dorsally in its lower part.

On the anterior surface the sacrum presents an extra foramen on the right side on the second vertebra, between the first and second foramina.

It is somewhat remarkable that all these specimens of supernumerary synchondroses of the sacrum should be on the left side.

[The numbers refer to specimens presented by Dr Ramsay Smith to the Anatomical Museum of the University of Edinburgh.]

RUDIMENTARY CONDITION OF THE CAROTID CANAL.

By G. H. K. MACALISTER, B.A., *St John's College, Cambridge.*

THE following peculiarities were observed in the skull of a male negro from Jamaica presented by Dr C. A. H. Thomson of Christ's College to the Anatomical Museum at Cambridge. The right side is normal, but the left side shows in its petrous region certain abnormalities associated with an anomalous carotid canal.

The jugular foramen is normal: its anterior border is coronal and has rather a sharp edge; its mesial border is situated lateralwise to the anterior condylar foramen. The region which is especially anomalous is situated anteriorly to the jugular foramen; its lateral boundary is formed by the ragged edge of the tympanic bone, and its mesial boundary is the basilar process of the occipital. The 'carotid lobe' of the petrous bone, which normally wraps around the carotid canal on its outer wall, is here a more or less quadrilateral plate, with a rough surface.

Along its mesial margin the bone is flattened. This flattened area forms a channel whose banks are formed by the mesial border of the remainder of the petrous bone laterally, and by the lateral edge of the basilar plate mesially. This channel continues backward, crosses the petro-occipital suture, and comes into relation with the mesial border of the jugular foramen; it terminates at the anterior condylar foramen. Continuing forwards, the channel leads to a tunnel which, running between the apical region of the petrous portion of the temporal bone and the great wing of the sphenoid, opens into the middle fossa of the cranial cavity. From this a small groove passes forwards between the lingula and the body of the sphenoid to the anterior clinoid process. It then passes over a solid formation, which corresponds to the united anterior clinoid process and olivary eminence—for, while in a normal sphenoid the carotid groove is sufficiently big to establish the independence of these two named processes, the minute substitute for the groove observed in this specimen is a mere trace on a solid bar of bone.

In the middle fossa the tunnel is separated from the hole for the petrosal nerves by a portion of the lingula, which projects backwards and meets the petrous portion of the temporal bone.

The petrosal portion of the channel described is 18 mm. in length and 4 mm. in width.   The tunnel is 3 mm. in diameter.

At the postero-lateral angle of the rough area described above as the carotid lobe of the petrous portion of the temporal bone is a foramen 0·7 mm. in diameter, which is probably the representative of the carotid foramen.   From this a tortuous canal runs first upwards and backwards, then forwards and inwards, coursing through the very midst of the cancellous structure of the petrous element towards its apex, where the canal opens a little below the point where a normal carotid canal should open.   This minute canal is at first circular in lumen, but becomes slit-like towards the apex.   It is 31 mm. in length, and in its circular portion is 0·7 to 0·5 mm. in diameter.

SOME PECULIAR FEATURES IN A TEMPORAL BONE.

By P. P. Laidlaw, *St John's College, Cambridge.*

A TEMPORAL bone presenting several unusual characteristics has been found in the collection of Egyptian bones in Cambridge University Museum.

The bone is of Egyptian origin in a good state of preservation, and has small portions of the sphenoid and occipital synostosed with it, but the rest of the skull is lost. The part of the sphenoid in question includes the spine and foramen spinosum,

View of specimen from below.—(i) Absence of stylo-mastoid foramen, large size of mastoid foramen. Styloid and zygomatic processes are broken. Note the shallowness of the digastric groove.

while the occipital portion, though larger, presents no feature worthy of notice: its extent and shape may be seen in the accompanying drawing. It belongs to the left side.

The peculiar features are:—

(1) Absence of the internal auditory meatus and of the stylo-mastoid foramen.

(2) Absence of the jugular fossa, and partial absence of the

lateral sinus-groove in the interior, with presence of a large mastoid foramen.

On the posterior intracranial face of the petrous bone the internal auditory meatus is absent, a minute hole being observable in the place where the large canal usually opens. This, on probing with a bristle, seemed to be occluded, and might be due to imperfect preservation of the inner table, as there are one or two other such imperfections in other parts, a rather more prominent set of holes being found on the surface of the *tegmen tympani*. Correlated with the absence of the internal
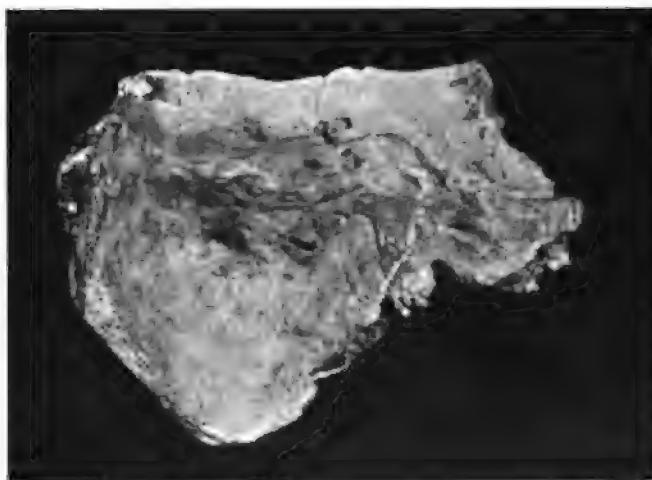
View of specimen from behind and above.

meatus is the absence of a stylo-mastoid foramen, and I was unable to find any foramen in the vicinity through which the facial nerve could have made its exit from the skull. As far as I know, absence of the internal meatus has not been met with hitherto.

The second peculiar feature is that the groove for the lateral sinus ends at the mastoid foramen, all the blood being evidently drained by this canal. The sigmoid groove of the lateral sinus is somewhat smaller than usual, and the foramen larger than normal. The superior petrosal sinus-groove is present in its normal form, but the inferior is absent.

One would expect that the absence of any internal auditory meatus, and therefore presumably absence of the VIII. and VII. nerves, would have so affected the development of the internal ear as to render it obviously imperfect. Such, however, is not the case in this instance, as the bony parts were well developed and, compared with a European bone taken at random, of large size.

Thus, such points as hiatus Fallopii, canal of Eustachian tube, and tensor tympani were apparently the same as usual, while the aqueductus cochleæ and aqueductus vestibuli were both easily identified.

Also such points as the *fenestræ rotunda et ovalis* of the internal wall of the tympanum could be identified by reflecting light down the external auditory meatus. In short, it otherwise presented perfectly normal features.

I append some measurements to compare with an ordinary well-developed temporal bone.

	Egyptian bone.	European.
From the tip of petrous bone to internal surface of skull-wall along the line of the superior petrosal sinus, ...	61 mm.	60 mm.
From the same point in the interior of the skull to the apex of the angle occupied by the spine of the sphenoid, ...	49 mm.	46 mm.
From the apex of angle in last measurement to the tip of the petrous bone, . . .	26 mm.	25 mm.

These give an anterior triangle, which expresses to a certain extent the development of the petrous bone and internal ear.

	Egyptian bone.	European.
From tip of petrous bone to the angle occupied by the jugular process of the occipital, . .	30 mm.	34 mm.
From internal surface of skull to where superior petrosal sinus meets it, . . .	46 mm.	35 mm.

Lastly, the vertical depth from the surface of the eminence of the superior semicircular canal to the base of the styloid process was 23 mm. in the Egyptian and 25 mm. in the European.

These figures do not indicate any imperfect development of the Egyptian specimen.

The specimen, on being sawn open, was seen to present a completely developed bony labyrinth, as all parts were present

as far as could be seen—vestibule, semicircular canals, and cochlea.

The cribriform area at the fovea hemispherica was easily made out with the aid of a lens.   The small aperture mentioned above, which existed in the place of the internal auditory meatus, proved to be a very imperfect aqueduct of Fallopius, which, however, could not be traced far ; moreover, the arrangement of the cancelli and lamellæ of the bone occupying the area usually taken up by the meatus showed that the condition could not be regarded as pathological.

NOTES ON A CASE OF FEATHER-BIFURCATION.

By W. J. RUTHERFURD, *University of Glasgow*.

FEATHERS, in common with other structures, are at times liable to show abnormal characters, the reasons for which can at most be only imperfectly understood. Feathers of birds, teeth of mammals, etc., and many other structures, as is well known, are all produced as epidermal growths having some connection with a mesoblastic papilla at the base of a follicle which is sometimes only secondarily formed.

Probably all such structures which are in connection with a single papilla or follicle have been observed at one time or another to present the condition of Dichotomy or, more generally speaking, of ' bifurcation ' as an abnormality.

It would seem that, as the tooth is the structure whose well-being or the reverse impresses itself upon the individual the most, dichotomised teeth have had more attention paid to them than have cases of dichotomy in other analogous organs. This is only natural, since so many isolated specimens must pass under the observation of dentists every day.

Bifurcated or ' double ' feathers have, however, been noted on several occasions, and if we knew where to look for recorded instances of the abnormality, quite a large amount of information might be collected in reference to this subject.[1]

I have had in my possession since the spring of 1901 a domestic pigeon which has in every ' crop ' of feathers presented two bifurcated rectrices—the feather nearest to the middle line on each side of the tail. When I first saw the bird, it was not many weeks old, and it then had the two bifurcated feathers in exactly the same place in which they have always been presented—they being the same two follicles which constantly give rise to this abnormal type of feather. I think it worth while mentioning this particularly, because many ornithologists lay great stress on the constant difference between the first

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[1] I have noticed that Bland Sutton mentions ' dichotomised feathers ' in his *Evolution and Disease* (Contemporary Science Series, No. v.), [1890]; and Gadow, in Newton's *Dictionary of Birds*, part iii. p. 587 (1890), mentions 'double feathers,' but without giving any information on the abnormality.

plumage, or nessoptiles of a young bird and that which it subsequently acquires; and, considering how they are apparently justified in drawing this distinction, it seems at first sight
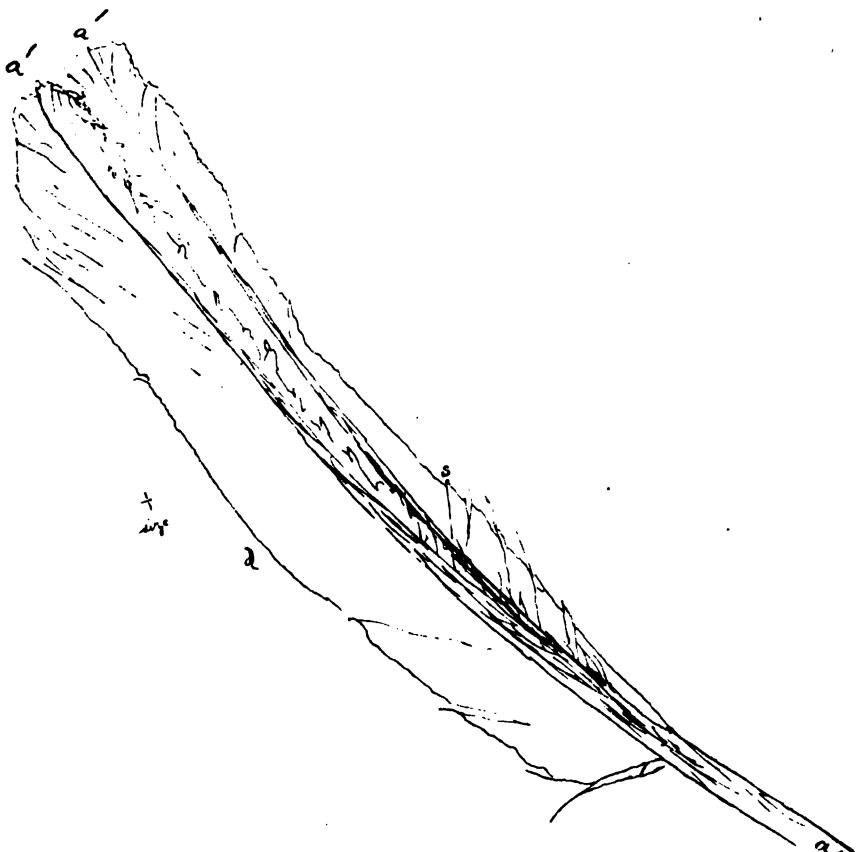
FIG. 1.—The two median rectrices of a 'domestic pigeon' showing dichotomy.
1. Feather to right of middle line seen from right side (*d*) and above—*a*, 'barrel'; *a′*, secondary shaft. 2. Feather to left of middle line (second type) seen from lower surface — *b*, 'barrel'; *b′*, secondary shaft; * Indicates where some of the filaments of the web are fused, forming a solid mass.

remarkable that an abnormality present in the nest-feathers of a bird should be reproduced feather for feather in after-life, while the colouring of the feather is, as I have noticed, by no

means consistently adhered to from year to year even in such birds as the pigeon, whose feather-pigmentation has been, as one might say, standardised in the course of many generations even in the case of the common or garden sorts about whose 'points' no care at all is taken.

It will be noticed from the accompanying sketch that the bifurcation is by no means equal in the two abnormal feathers of the same year, and I may mention that the feathers which grew at the end of the summer of 1902 are those which I have figured here. The bifurcated portion of each feather shows four 'webs' instead of the normal two, and in this, as in other respects, the feathers merit the title of 'double feathers.' The additional webs in apposition to one another are pointing up-wards to meet at an angle like the sloping ridges of a roof, and are much worn and somewhat irregular in outline from their constant mutual friction. The separate filaments of which these webs are formed are stiff and bristle-like, though bearing the ordinary barbules as might be expected; distally, however, they are quite normal, and have only been affected by friction to a very slight degree. Some of these filaments of the additional or secondarily formed webs, just in the angle between the two 'secondary shafts,' as I will call them, where they come off from the main shaft, are exceedingly small and incon-spicuous; while others (some on that secondary shaft which was nearer to the middle line, others on that which was more remote) are unusually long and thick (I have measured several which are 14 to 17 millimetres in length) and these again may have small secondary filaments coming off from them at a slight angle.

In this year (*i.e.*, 1902) the bifurcated feathers were of two distinct types: the one, which grew to the right of the middle line, had its shaft (using this word in its limited meaning of the part of the 'quill' which has a web coming from either side—right and left—of it) doubled in practically the whole of its length, the only part of the 'shaft' common to both the secondary shafts being one centimetre long; while the other—from the left side of the middle line—has a common shaft 46 millimetres in length, each of its secondary shafts being 62 millimetres long.

The secondary shafts of the more markedly double of the two feathers under consideration have the following lengths :—

> that nearer the middle line 107 mm.,
> that farther off from the middle line barely 109 mm. ;

there being thus a difference of not 2 millimetres between the two—a difference so small that it may be quite neglected.

FIG. 2.

It will thus be seen that the *only* difference between the two feathers, the total lengths of whose shafts are practically the same (12 cm. in the one case, and 11 cm. in the other), is the degree to which the dichotomy has been carried out, and this degree varies slightly, not only in the different feathers (from opposite sides of the mid-line, that is to say), but also in the same feather in different years (of course this means feathers from the same relative situation in the line of the rectrices, the amount of dichotomy to be seen in any two feathers from the same feather-follicle not being the same).

On cutting the shaft of the more markedly dichotomised of

FIG. 3.—Transverse section of common portion of shaft, showing its internal aspect, and bifurcation into the two secondary shafts.

the two feathers across at the place where it is supposed to become metamorphosed into the barrel, and looking up it

towards the free end of the feather, a distinct view was obtained of the double lumen, where the two secondary shafts came off from the main or parent stem.

I particularly noticed that the two dichotomised feathers which grew in the room of those which had just moulted towards the end of August of 1901 (this was the second crop of feathers, or the first crop of teleoptiles), were much less markedly dichotomised than either before or since, the dichotomy only extending for about 5 centimetres or even less from the distal extremity of each of the two feathers under consideration.

At this time I happened to notice in the case of one of these feathers a condition which I then thought offered a clue to the whole condition. The abnormal feather situated on the right side of the body was, during its growth till the entire feather was between about 4 or 5 centimetres long, soaked and discoloured with blood and pus. A little reflection, however, soon convinced me that this condition was only the effect, and not the cause, of the dichotomy, and could not be expected to occur with each of the feathers every time a dichotomised one was in the process of development and growth. The reason of the sepsis was probably as follows :—The feather-follicle was no doubt normal in size, and with a lumen only adapted for the passage of a normally sized feather; it would consequently become injured (as was indicated by the blood-stains) by the passage of what was, for this purpose, practically two feathers, and a micro-organism would subsequently gain admittance to the abraded surface.

I have satisfied myself that the abnormality does not in this instance arise from the fusion of two of the growing rectrices because of over-crowding or any other cause, by the simple procedure of counting the number of rectrices. For the domestic pigeon, and, in fact, for all the *Columbidæ*, this number is twelve, and by counting each abnormal feather as a single one, I arrive at that number for this bird, which has thus the normal number of tail-feathers.

The reason of the abnormality is at present quite unknown to me, with the exception that in all probability it is *not* due to domestication. It is very easy to put all departures from the

normal down to 'the evil effects of domestication,' as it is the modern tendency to do; but it is just a lazy man's trick, unless the procedure can be proved up to the hilt, which is seldom possible. As Gadow says, "monstrosities are naturally more *observed* in domesticated than in wild birds";[1] but it must be borne in mind that the effect of domestication is, by bringing the domesticated animal more into contact with man, just to make every little departure from the normal the easier of observation and of perpetuation, while in the natural condition every such departure has enormous odds in the favour of it not being noted by anyone, and of being in subsequent generations swamped by the succeeding increments of normal blood. This is a fact that some modern theorisers would do well to remember. Canon Tristram has kindly informed me that he has noticed a similar case of bifurcated feathers on the skin of a foreign hawk: the abnormalities are similar in each case, though in the one instance the bird is domesticated, while in the other case the bird was what is (for some unknown reason) called 'wild.'

It would have been interesting in many ways if I could have obtained young birds descended either from this bird or from its blood relations, but, unhappily, the bird itself seems to be quite sterile, and the stock from which I obtained this individual has subsequently been dispersed.[2]

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[1] *Loc. cit.*; the italics are mine.

[2] It would be well here to quote in full a passage from Darwin's *Variation of Animals and Plants under Domestication*, where, although his meaning is not as clearly worded as might be desired, he refers to a similar condition. He writes: "With respect to the primary wing-feathers, the number in the *Columbidæ*, as far as I can find out, is always nine or ten. In the Rock-pigeon it is ten ; but I have seen no less than eight short-faced Tumblers with only nine primaries, and the occurrence of this number has been noticed by fanciers, owing to ten flight-feathers of a white colour being one of the points in short-faced Baldhead-Tumblers. Mr Brent, however, had an Air-Tumbler (not short-faced) which had in both wings eleven primaries. Mr Corker, the eminent breeder of prize carriers, assures me that some of his birds had eleven primaries in both wings. I have seen eleven in one wing in two Pouters. I have been assured by three fanciers that they have seen twelve in Scanderoons ; but as Newmeister asserts that in the allied Florence Runt the middle flight-feather is often double, the number twelve may have been caused by two of the ten primaries having each two shafts to a single feather" (vol. i. p. 159). It will be noticed that this explanation offered by Darwin is only a supposition of his own, and it would be interesting to learn whether it was correct or not.

I do not know that, in the present state of my knowledge on this subject, it is permissible for me to draw any deductions on the subject of the number and even the arrangement of feathers, but since Darwin gave an explanation for the presence of extra wing-feathers in certain pigeons, I think that a similar explanation might be advanced for the enormous number of additional rectrices present in many fantails [1]—that the extra number was arrived at by the successive differentiation of single rectrices into several complete feathers, or even into groups of feathers.[2] This might even be applied to those aberrant members of the *Columbidæ*, where the number of rectrices is more than normal.

Darwin also mentions, in connection with those pigeons with excess of rectrices, that the uropygial gland is aborted in many instances.[3] I will endeavour, if my bird by any mischance should happen to die while I am still interested in this subject, to investigate by sections the state both of its oil-gland and of the papillæ and follicles from which the abnormal feathers ' are wont' to arise. It strikes me as being somewhat curious that in the *Columbidæ* the absence of the uropygial gland should be connected with an increase in the number of the rectrices, when the same absence is found conjointly with an aborted state of the rectrices in certain ' tail-less' fowls.

I may find that the dichotomy is due to a compound papilla upon which the feather rests. Such compound papillæ are given the credit of causing the tubercles normally found upon tri-tuberculate as well as upon multituberculate teeth, and will, perhaps, be used to explain the abnormal condition shown by dichotomised or bifurcated feathers (I give a choice of terms, so that, if the first happens to be open to criticism, the second may escape).

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[1] *Loc. cit.*, pp. 146-7, 161-2, etc.

[2] This opens up a tempting field for speculating on the origin of pterylæ, etc., especially when taken in connection with recent investigations on hair-grouping in relation to reptilian scales.

[3] *Loc. cit.*

ON THE OCCURRENCE OF A 'PRINCIPAL ISLET' IN
THE PANCREAS OF TELEOSTEI. (Preliminary Note.)
By JOHN RENNIE, B.Sc., *University Assistant in Zoology,
Aberdeen.*

OUR knowledge of the existence of islets of epithelial cells
in the pancreas of fishes is of comparatively recent date
(Laguesse, '95 ; Massari and Diamare, '98), and has hitherto
been limited to a relatively small number of species. In an
account of work soon to be published I describe them in all
the leading divisions of Teleostei, where they are shown to occur
with such frequency that one may now conclude they constitute
a common anatomical character of that group. In this investi-
gation some facts of interest have emerged, one of which is the
subject of the present note.

As the result of the examination of large numbers of
specimens, I have noted in various species the constant occur-
rence in a definite position of a particular islet. Of the islets
present, as far as my observation goes, this one is invariably the
largest, and its position in the different species in which I have
found it is so similar, that I am of opinion it is to be regarded as
the same organ in all cases. Since I have not been able to
discover (with one possible exception noted below) the same
constancy in the case of the other islets, and since it is quite
evidently the most important of these formations, I have termed
it the 'principal islet.' Owing to the extremely diffuse con-
dition of the pancreas in most Teleostei, these islets, possessing
greater opacity, may usually be observed by the naked eye.
They differ somewhat in form, but I have always found the
principal one rounded or oval in section and enclosed within
a more or less definite capsule. In *Pholis gunnellus*, the species
of perhaps smallest adult size in which I have noted its existence,
its longest diameter is about 1·5 mm.; while in large *Cyclopterus*
or *Lophius* it may reach 14 mm. in length and 5 mm. in thick-
ness.

The following is a list of the species in which I have observed
it, viz. :—*Zeus faber, Lophius piscatorius, Cyclopterus lumpus,
Pholis gunnellus, Zoarces viviparus, Anarrhichas lupus, Chiro-*

lophis galerita, Hippoglossus vulgaris, Pleuronectes platessa, Syngnathus acus, Nerophis æquoreus, Syphonostoma typhle. Besides these I have further noted in several *Gadidæ* and other *Pleuronectidæ* a structure similar in appearance, which is probably this islet, but I have not yet been able to verify its constancy nor to examine it histologically.

In *Zeus, Pleuronectes,* and *Hippoglossus* the principal islet is attached to the base or side of the gall-bladder. In the first two it is more or less completely enveloped by zymogenous tissue, in *Hippoglossus* the latter is almost absent. In this position Diamare has noted the occurrence of a large islet in *Orthagoriscus molæ* and in *Rhombus lævis,* but makes no observations on their constancy. In the other species which I have

Principal Islet in *Pholis gunnellus. l.,* liver ; *sp.,* spleen ; *m.a.,* mesenteric artery ; *he.a.,* hepatic artery ; *po.v.,* portal vein ; *pr.is.,* principal islet.

named it may be stated generally that this islet is placed on the ventral side of the mesenteric artery and near to it, in the region of the abdominal cavity anterior to the spleen. In the forthcoming communication already referred to I shall indicate its exact position in each case ; at present I shall limit myself to a statement of its relations in *Pholis gunnellus.* This species, though small, is one in which it may very readily be found. If the abdominal cavity be laid open by removing the right wall and the specimen pinned to a dissecting tray under water, the viscera may then be drawn towards the ventral side of the fish. If this be done, the leading blood-vessels, owing to their walls being pigmented, may easily be followed. A short distance in front of the spleen the mesenteric and hepatic arteries, together with the portal vein, enclose quite a small

triangular area, within which lies the islet in question. It is enclosed in a fairly tough capsule, which is frequently quite black owing to the deposition of pigment. (See figure.) Histologically it possesses the same structure as other islets in the same and other fishes, and no doubt can be entertained as to its homology. The authors cited have come to the same conclusion regarding similar formations seen by them. Before becoming acquainted with their work, I had satisfied myself as to this, their true nature; my evidence will appear in my next communication.

Regarding the question of function much has already been written on the subject, mainly with regard to the higher vertebrates. Latterly the consensus of opinion inclines to the view of an internal secretion, and with this view my observations are in complete accordance. The opinion of Laguesse, that they represent a stage to which the zymogenous elements may revert for a time, the tissue alternating throughout life between the epithelial and zymogenous conditions, does not agree with the facts in those fishes in which this particular islet—apart from others—is to be found at all times. It is a permanent organ, and I hope to show from experiments at present in progress, as well as from internal histological evidence, that it is functionally active.

I have further given some attention to the question of a possible similar constancy of occurrence in the case of the other islets. For this purpose I have examined several hundreds of *Lophius piscatorius* and a smaller number of *Hippoglossus vulgaris* (about fifty). In both of these I selected a small area of pancreas close to the pylorus. Within this area in *Lophius* there are situated several islets—a varying number, I am inclined to think. *With very great regularity* there occurs one which is markedly larger than the others. It is always next in size to the principal islet. I think it probable that more careful observation will show that it occurs with the same constancy as the principal. In *Hippoglossus* the area contained one large visible islet. It and the principal were the only two I could find by dissection in this species. In every case, save one or two, it was found. Whether the failure to find it in those few cases was due to want of skill on the part of the investigator

will be revealed by more extended enquiries. I incline to the view that it also is a structure constant in occurrence, with definite anatomical relations.

Further, I have found an islet, large enough to be seen by the unaided eye, within this area, in *Anarrhichas, Pholis,* and *Pleuronectes*; I have not yet had opportunities for observing whether it occurs regularly or not.

If constant and variable islets can be proved to exist, the relation between the two, I suggest, is probably similar to that between the thyroid and accessory thyroids, or spleen and accessory spleen. If this is so, since no constancy of the nature I describe has, so far as I know, been found amongst higher vertebrates, it may be that in the course of phylogeny the principal islets have disappeared, while the accessory have increased in number and importance.

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ON A METHOD OF PREPARING THE MEMBRANOUS
LABYRINTH. By ALBERT A. GRAY, M.D., F.R.S.E.

OUR anatomical knowledge of the soft parts of the internal ear has been obtained not by observations made upon the organ as a whole, but by piecing together the appearances seen in fragments. It is nothing short of astonishing how anatomists have been able to do so with such accuracy. Nevertheless such a state of matters is in the highest degree unsatisfactory, for it means that few anatomists will be willing to spend the requisite time to acquire their knowledge from nature, and no preparations, so far as I know, exist from which students can learn the subject in the same way. Furthermore, it is in human nature to desire the view of any object in its entirety, not as broken fragments.

Several methods have been described with the object of obtaining the labyrinth as a whole, but they seem to have failed, and in my experience of them they failed completely.

At intervals during the past two years I have made many attempts in various directions, but only recently have I found out a method which can be depended on to give certain results.

The general principle of my method is to embed the whole pyramid of the temporal bone so thoroughly that no acid can affect the soft parts, then to decalcify and *disintegrate* the bone so completely that no force whatever is required to remove the destroyed tissue surrounding the labyrinth, and finally to remove the embedding material in such a way that the membranous labyrinth is left uninjured.

The pyramid of the human temporal bone is removed from the base of the skull in the post-mortem room. The superfluous bone is removed with a saw; the stapes is carefully extracted from the oval window, and a small hole is filed in the superior semicircular cánal. The structure is then immersed in 90 per cent. alcohol for at least a fortnight, the alcohol being frequently changed. It is then transferred to absolute alcohol, where it remains at least a fortnight, this alcohol also being frequently

changed. During this period it must be kept in a glass stoppered jar. The alcohol obtained from the chemist is not really absolute; it may be made so, however, by putting an ounce of anhydrous sulphate of copper to every pound of alcohol. When wanted for use, the clear alcohol at the top is poured off as desired, care being taken that the sulphate of copper does not pour out along with it.

From absolute alcohol the bone is removed quickly to xylol, where it again remains at least a fortnight, the xylol being frequently changed. I find that if a vacuum, more or less complete, be made now and then in the jar above the level of the xylol, diffusion occurs much more rapidly and completely. I do this by fixing an india-rubber cork, with a glass tube through it, into the mouth of the jar, and extracting the air and gases through a rubber tube connected with a small air-pump.

From the xylol the bone is removed to melted paraffin of a melting-point of 52° C. or 54° C. The paraffin must be changed two or three times during the fortnight which must be allowed for the embedding. This is important to the success of the method; the paraffin must permeate the soft parts far more completely than is necessary in the case of embedding for microscopic section purposes. I frequently make use of the air-pump to produce a vacuum above the melted paraffin, but sometimes the latter solidifies during the process; this, however, does not appear to affect the ultimate result. Of course the temperature of the paraffin stove must not be allowed to rise above 55° or 56° C.

After the bone has been in the paraffin bath for a period ranging from two to three weeks, the paraffin is cooled as quickly as possible and the bone cut out from the block. The superfluous paraffin is then carefully scraped off the bone and decalcification is proceeded with.

For this purpose neither nitric nor hydrochloric acid by itself is suitable; they should be mixed. The solution I use consists of 2 parts pure nitric acid, 2 to 3 parts pure hydrochloric acid, and 6 to 18 parts water; the nitric acid should be mixed with the water first, and the hydrochloric acid added.

The bone is put into a large quantity of this mixture and suspended near the top by fine twine. The mixture should be

frequently changed, and in about three weeks or a month decalcification and disintegration will be complete. It will be found that while the cancellous portions of the bone are still firm, being supported by the paraffin, the dense bone which surrounds the labyrinth will have become quite pulpy ; indeed the labyrinth should lie almost loose in the pulp; if this is not so, the preparation should be put back into the acid and left longer, and the solution should be made stronger by adding a little more hydrochloric acid.

After decalcification the mass should be thoroughly washed for twenty-four hours in gently running water, care being taken that it does not get roughly handled during the process.

Some of the cancellous portions of the bone may now be picked very carefully away with the point of a sharp knife, and then the mass is carefully removed to absolute alcohol, where it remains for about ten days, the alcohol being changed several times. From the alcohol it is transferred rapidly to xylol, which slowly dissolves out the paraffin and leaves the membranous labyrinth transparent. Surrounding portions of cancellous tissue may be slightly adherent, but they can be separated by fine sharp scissors as the structure lies in the xylol. If the dehydration has been thorough, the extremely delicate structures do not collapse or shrink when the paraffin is removed. The specimen is preserved in xylol in the glass jar when the paraffin has been melted out. The courses of the various portions of the nerves stand out very plainly, and may be shown still more clearly if the specimen has previously been stained and fixed with osmic acid.

Very pretty specimens may also be made by injecting the endolymph spaces (before hardening) with carmine gelatine, the injection being done through the aqueductus vestibuli.

The blood-vessels may be injected through the internal auditory artery, also of course before hardening.

TWO HEARTS SHOWING PECULIARITIES OF THE GREAT VEINS.

By DAVID NABARRO, M.D., M.R.C.P., *Assistant Professor of Pathology, University College, London; Pathologist to the Evelina Hospital for Children, Southwark.*

THE two specimens described in this paper were exhibited at the meeting of the Anatomical Society held on July 3rd, 1902, and as they show rare abnormalities of the great veins, I have thought it expedient to record them. Both occurred in patients at the Evelina Hospital for Children, under the care of Dr F. Willcocks.

A. The first specimen is that of a heart in which all the pulmonary veins opened into the right auricle through a large coronary sinus.

The patient, a female child aged 5½ months, was admitted into hospital on April 18th, 1902.

The history is as follows:—The child was born prematurely (at 8 months). At first nothing special was noticed about her colour, but when 3 months old she used to wake screaming and fighting, as though to get her breath, and went 'black' in the face on those occasions. She had three or four of these attacks in the day. The baby was noticed to be wasting about one month before admission, and during this time she suffered also from bronchitis. The lips and extremities were of a blue colour during the last four weeks of life. Bulging of the præcordium was obvious to inspection three weeks before admission, and increased up to the time of admission into the hospital. Apparently the child seemed easier when lying on its stomach or against the nurse's chest. After the attacks of cyanosis the face is said to have been swollen, and on the day before admission the feet were also swollen. The child was breast-fed until admitted to hospital.

Condition on admission.—The child was small, but fairly long, and of very slender build; 20½ inches long and 13½ inches round the chest. Cry feeble; breathing very rapid (about 68 per minute) and apparently ineffectual, though attempts were made

at deep breathing. The eyebrows were raised with inspiration, and the child yawned occasionally. The skin was of a dusky tint, the lips blue (rarely reddish), the veins of the fingers large, the finger-tips cyanosed and beginning to show clubbing. Slight œdema of the feet was present.

The chest was barrel-shaped, and moved very little with respiration. There was obvious fulness in front, especially in the præcordial region. The heart's impulse could not be felt. The area of cardiac dulness was increased, extending upwards to the 2nd intercostal space, outwards 1½ fingers-breadth beyond the nipple line and to the right border of the sternum, probably not beyond. On auscultation, the heart sounds had a 'galloping' rhythm, and a loud murmur, probably systolic in time, was heard, best in the nipple line. Elsewhere the sounds were 'distant.' There was some suspicion of a tricuspid regurgitant murmur. The right lung was apparently normal, except for crepitations at the base. The left side of the front of the chest was scarcely resonant at all.

While in hospital the child was constantly blue and cold. T. rarely above 97° F.; breathing very rapid; pulse weak and running. She remained in much the same condition until the 22nd April, when taken worse, and she died at 4 a.m. on the 23rd.

The autopsy was done about twelve hours after death.

On opening the body in the ordinary way, the pericardium was seen to be very big, the thymus small, and the left lung was not visible at all. The heart was 'globular' in shape, and the whole of the anterior surface was constituted by the right ventricle. The interventricular furrows were present, and the left ventricle seen to be small. The aorta was considerably narrower than the trunk of the pulmonary artery. The ductus arteriosus was easily dissected out, but was very small, and on subsequent further dissection found to be impervious, only a depression being present in the interior of the pulmonary artery where the ductus arteriosus was given off. The large branches of the aorta were normal. The superior vena cava was considerably smaller than the inferior. Both cavæ ended normally in the right auricle, which was very much bigger than the left.

The right auricle, on being opened up, was seen to be considerably

larger than normal (fig. 1). Its walls were much thickened and hypertrophied. The auricular appendix was very well developed, and its walls had prominent musculi pectinati. A well marked Eustachian valve was present in front of the orifice of the vena cava inferior, and the inner cornu of the Eustachian valve was continuous with the anterior limb of the annulus of
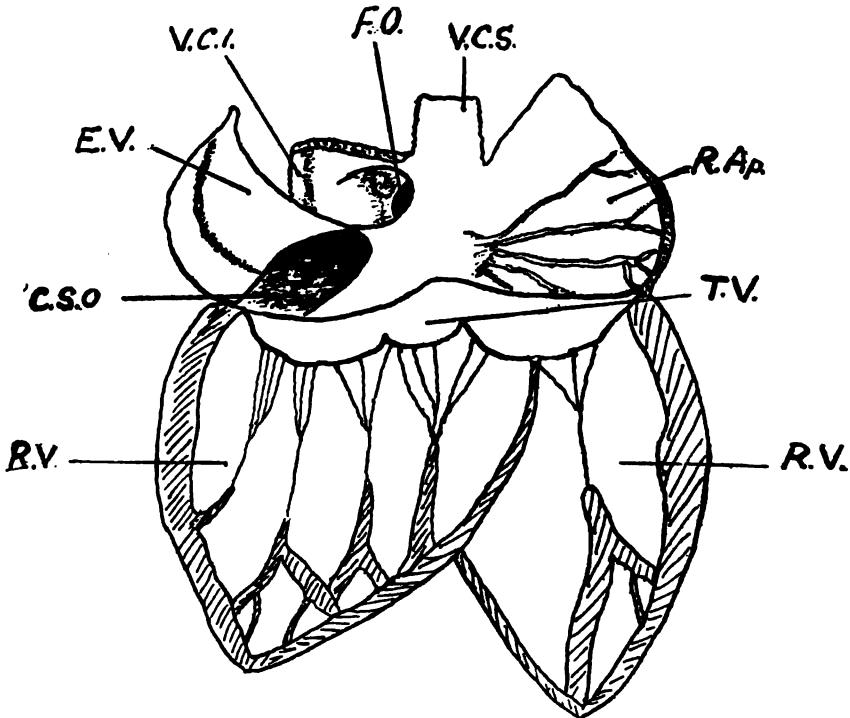
Fig. 1 (Case A.).—Semi-diagrammatic view of right auricle and ventricle. R.V., right ventricle (cut open); C.S.O., opening of enlarged coronary sinus into right auricle; E.V., Eustachian valve; V.C.I., inferior vena cava (cut open); F.O., foramen ovale; V.C.S., superior vena cava (opened out); R.Ap., right auricular appendix; T.V., flaps of tricuspid valve.

Vieussens. The interauricular septum was well formed, only a small slit-like foramen ovale (3 mm. by 1·5 mm.) being present. In the situation of the orifice of the coronary sinus was a very large oval aperture, bounded by the annulus Vieussenii, the Eustachian valve, and the auriculo-ventricular ring.

This aperture (fig. 1, C.S.O.) was subsequently seen to lead from an abnormally large coronary sinus into the right auricle. On slitting up the openings of the four pulmonary veins, an irregularly quadrilateral cavity (fig. 2) was discovered, which was at first thought to be a part of the left auricle, shut off by a septum from the main body of the auricle and the appendix.
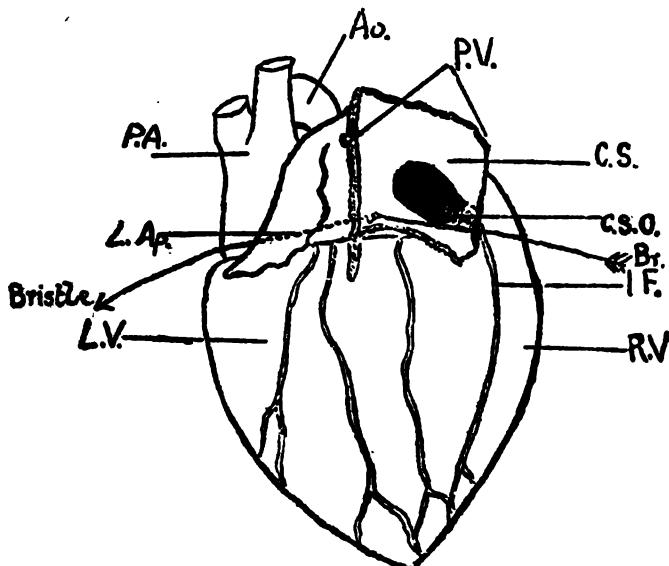

FIG. 2 (Case A.).—View of the heart from the left and behind, showing the enlarged coronary sinus (receiving four pulmonary veins and the great cardiac vein). L. V., left ventricle ; L.Ap., left auricular appendix—(to its right in the figure is the small left auricle unopened) ; P.A., pulmonary artery ; Ao., aorta ; P.V., orifices of the pulmonary veins ; C.S., coronary sinus ; Br., bristle passed through the orifice of the great cardiac vein ; C.S.O., opening of coronary sinus into right auricle ; I.F., posterior interventricular furrow ; R.V., right ventricle.

Closer study of the anomaly, however, showed that this cavity had no connection with the left auricle, but was really a big coronary sinus, into which the pulmonary veins opened. Two facts indicate clearly that this cavity is really a dilated coronary sinus: (1) the opening into the right auricle, although much larger than normal, is in the situation of the orifice of the coronary sinus of the heart; and (2) the great cardiac vein opens into this sinus (a bristle is passed through this orifice,—see fig. 2).

The right ventricle was much larger than normal, and its walls greatly thickened. There were well marked columnæ carneæ, the tricuspid valve was normal, as were also the chordæ tendineæ. The pulmonary artery was larger than usual, but was otherwise normal, the three semilunar flaps looking quite healthy. The trunk of the pulmonary artery soon divided into the two main branches, and at a distance of about 18 mm. from the commencement of the arterial trunk was a small depression in the wall of the vessel, indicating the origin of the ductus arteriosus, which, however, was completely obliterated.

The left side of the heart was seen to be but poorly developed. The left auricle, not being fed by the pulmonary veins directly, was a small cavity (see fig. 2), to which a small appendix was attached. The only entrance into the left auricle was from the right auricle, by way of the slit-like foramen ovale. The left ventricle was small. The smoothness of the walls was a noticeable feature, hardly any trabeculæ being present. The mitral orifice appeared normal in structure, but was on a diminutive scale, the cusps, chordæ tendineæ, and the musculi papillares being all much smaller than on the right side. The left ventricular wall was thinner than the right. The aorta, which was considerably smaller than the pulmonary artery, was given off by the left ventricle, and was furnished with a valve of three semilunar flaps as usual.

The heart, with a short length of great vessels attached, weighed 59 grammes, or more than double the weight of a normal heart of a child of the same age.

Physiologically, this heart is of considerable interest, for it appears that all the blood for the systemic circulation had to pass through the small foramen ovale; and further, the left side of the heart never received pure arterial blood, unless some disposition of the valves and orifices directed the current of arterial blood from the dilated opening of the coronary sinus through the right auricle to the foramen ovale, and so straight into the left auricle. There is no evidence that such was the case. The circulation would probably have been as follows: Venous blood from all parts of the body (except the heart itself) entered the right auricle through the two cavæ. Arterial blood from the lungs entered the dilated coronary sinus through the

pulmonary veins, and mixed with the venous blood from the heart brought in by the cardiac veins. This arterialised blood flowed through the orifice of the coronary sinus into the right auricle, and presumably became intimately mixed with the venous caval blood. The mixed blood flowed partly into the right ventricle, to be sent to the lungs, and partly into the left auricle through the very small foramen ovale, and so to the left ventricle. In this way the left side of the heart and the systemic circulation must have received a smaller quantity of blood than the right heart and the pulmonary circulation. This is evidenced by the smaller size of the left auricle, left ventricle, and aorta, as compared with the right auricle, ventricle, and pulmonary artery.

Another possible explanation of the great size of the right ventricle is that this chamber had to do the work of both sides of the heart. If tricuspid regurgitation were actually present (as was thought to be possible during life), then the systole of the right ventricle, besides driving blood to the lungs through the pulmonary artery, would have forced blood back into the right auricle, and through the foramen ovale into the left auricle.

It is interesting to note that the ductus arteriosus is not patent. That the child lived for nearly six months under such conditions seems remarkable.

The origin of the anomaly is to be explained as follows : Normally, the pulmonary veins grow into the mesocardium, and join into a common sinus which opens into the left auricle near the septum. In this case the aperture of the sinus of the pulmonary veins, instead of adhering to and opening into the back of the left auricle, seems to have formed its attachment a little lower down, and thus to have formed an opening into the part of the sinus venosus which normally forms the coronary sinus.

B. The second specimen is that of a heart showing a persistent left superior vena cava, which was joined by a left hepatic vein.

The patient, a male child aged 3 months, was admitted into hospital on August 29th, 1901, suffering from pneumonia, to

which he succumbed on Sept. 9th. During life no abnormality
of the vascular system was suspected.

The post-mortem examination was made fifteen hours after
death. The right lung was pneumonic, the left emphysematous.

Just before removing the heart from the body it was seen
that the left innominate vein, instead of crossing over as usual
to join the right innominate, was continued down as a left
superior vena cava, rather smaller in calibre than the corre-
sponding vessel on the right side. It passed down in front of
the root of the left lung, crossing the aortic arch just beyond
its junction with the ductus arteriosus, and then disappeared
behind the left auricle, lying in a groove between the left auricle
proper and its appendix (see fig. 3) A transverse jugular vein
(in the situation of the normal left innominate vein) was not
seen, but was not specially looked for.

The azygos veins and their tributaries were carefully dissected
out, with the following result (see fig. 4). On the right side
the vessels were normal, and the great azygos formed the
usual arch before its junction with the superior vena cava.
On the left side, the highest intercostal vein could not be
traced. The 2nd, 3rd, 4th, 5th and 6th united to form one
trunk (representing the left upper azygos and the superior
intercostal veins), which arched over the root of the left lung
and joined the left superior vena cava. The 7th, 8th and 9th
intercostal veins formed another trunk, which crossed the spine
and entered the right azygos. The other intercostals could not
be traced with any certainty. It was at the lower end that
this persistent left cava was most interesting. A probe passed
down the vessel was found to go directly into a left hepatic
vein, a vessel of considerable size, coming from the left lobe of
the liver, and not communicating with the other hepatic veins.
This left hepatic vein was joined by a vein from the left side
of the diaphragm (see figs. 3 and 4).

As far as they were examined, the other veins in the body
were normal. I regret, however, that I omitted to search for a
ductus venosus, or any remnant of it.

The heart was then removed from the body and opened in
the usual way. The right auricle showed, in the position of
the normal aperture of the coronary sinus, a large oval opening,

by which blood entered from the left superior cava. There was a small foramen ovale in the auricular septum. Entering the inferior vena cava are séen three hepatic veins—two very large and one small (see figs. 3, 4).

The left superior vena cava was next slit down, also the left hepatic vein and the intervening cardiac chamber (see fig. 3).
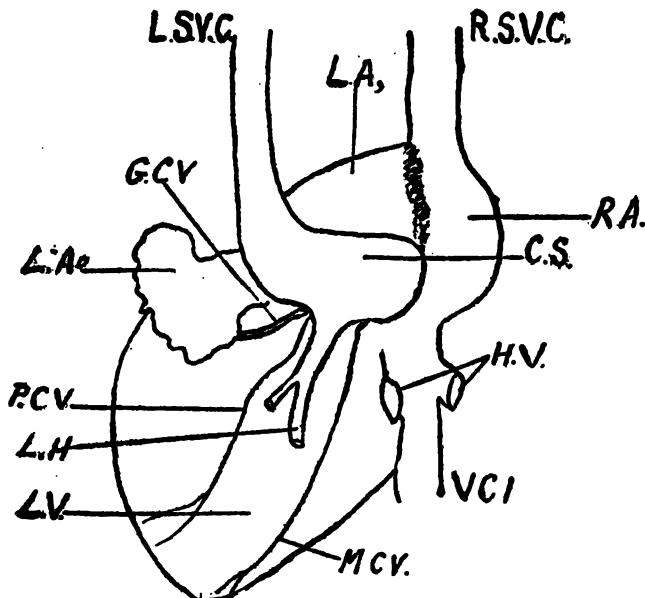

FIG. 3 (Case B.).—View of the heart from the left side and behind, showing the enlarged coronary sinus receiving the left superior cava, a left hepatic vein, as well as the great and middle cardiac veins. L.S.V.C., left superior cava; L.A., left auricle; R.S.V.C., right superior cava; R.A., right auricle; H.V., hepatic veins; V.C.I., inferior vena cava; L.H., a left hepatic vein; P.C.V., large posterior cardiac vein; M.C.V., middle cardiac vein; G.C.V., great cardiac vein; L.Ap., left auricular appendix; C.S., coronary sinus; L.V., left ventricle.

This, which is a true sinus venosus, is a small chamber with smooth walls, opening into the right auricle by the large oval aperture mentioned above. Near this opening and just above the auriculo-ventricular groove is a small hole through which the blood from the great cardiac vein flowed. In the wall of the cut left hepatic vein is seen the orifice of the left phrenic vein (see fig. 3).

The left auricle, the ventricles, aorta, and pulmonary artery were all normal.

The abnormal condition of the veins found in this case is
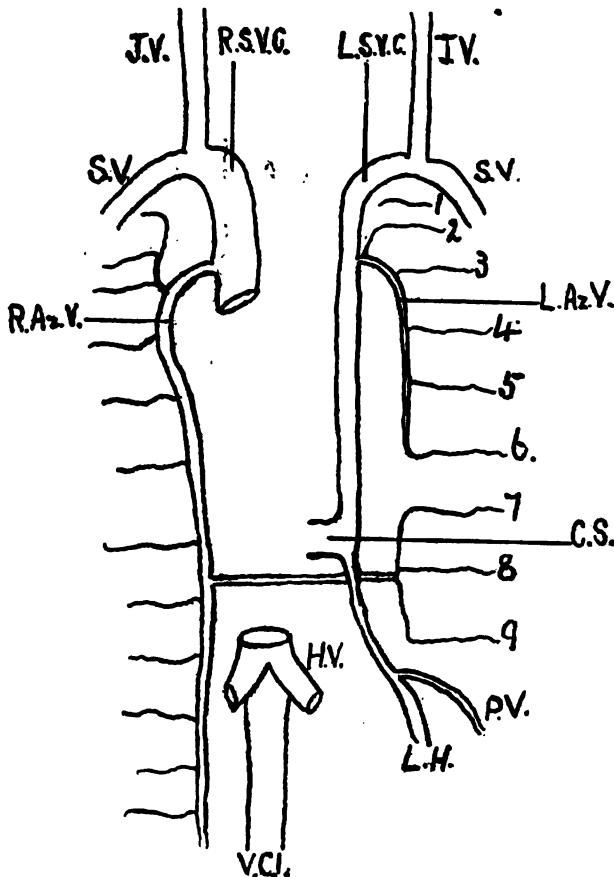
FIG. 4 (Case B.).—Sketch of the principal veins, showing the left superior cava and the disposition of the intercostal and azygos veins. R.S.V.C., right superior cava ; J.V., jugular veins ; S.V., subclavian veins ; R.Az.V., right azygos vein ; H.V., hepatic veins ; V.C.I., inferior vena cava ; L.H., a left hepatic vein ; P.V., a left phrenic vein ; C.S., coronary sinus ; L.Az.V., left upper azygos vein ; L.S.V.C., left superior cava.

readily explained by reference to what is known of the development of these vessels. Examples of a persistent left S.V.C. or duct of Cuvier are recorded from time to time, but it is

apparently very rare to find the left hepatic vein piercing the diaphragm and entering the left horn of the sinus venosus with the left duct of Cuvier, as is the case in this specimen.

In an early stage of development (about 4th week in the human embryo) two superior venæ cavæ (right and left) and an inferior cava open separately into the sinus venosus. Normally, the left duct of Cuvier with the left horn of the sinus venosus becomes obliterated, with the exception of a small part forming the definitive coronary sinus of the heart, while the right duct of Cuvier persists as the superior vena cava, and the right horn of the sinus venosus becomes incorporated with the cavity of the right auricle. At a rather earlier stage (about $3\frac{1}{2}$ weeks in the human embryo) the sinus venosus received a superior vena cava at each extremity, also two omphalo-mesenteric veins. The superior V.C. on each side receives the primitive jugular and the cardinal veins. In this case the arch of the left cardinal vein, instead of being obliterated as usual, persists as the arch of the left azygos vein.

The omphalo-mesenteric veins, opening directly into the sinus venosus, become the hepatic veins, and normally these all join up on the right side and enter the inferior V.C. The direct communication of the left hepatic vein with the sinus usually becomes obliterated early, but in this case it has persisted, and entering with the left duct of Cuvier, forms a persistent left horn of the primitive sinus venosus.

THE GENERAL CHARACTERS OF THE CRANIA OF THE PEOPLE OF SCOTLAND. By Sir Wm. Turner, K.C.B., F.R.S.

In November 1902 I communicated to the Royal Society of Edinburgh a Memoir on the Craniology of the People of Scotland, in which I described the anatomical characters of 176 skulls.[1] The skulls were collected in known localities, from Shetland in the north to Wigtownshire in the south, and from Iona and Stornoway in the west to Dunbar in the east; but as the majority were gathered in the counties south of the Clyde and the Tay, the memoir is more especially descriptive of the people of Lowland Scotland. In one of the chapters of the memoir I gave a general summary of the characters of the series of skulls; and in order to bring the conclusions arrived at in their study before a wider circle of readers, I have reprinted it in this number of the *Journal*.

General Survey of the Characters of Scottish Skulls.

In the preceding sections of the Memoir the characters of the skulls obtained in the several Scottish counties have been described in some detail. In this chapter it is intended to look at them as a whole, with the view of elucidating the form, dimensions and proportions which prevailed in the crania generally. I have endeavoured to group them according to sex; and though in the great majority I have succeeded in distinguishing the skulls of the men from those of the women, it is not unlikely that, like other craniologists, I have had to deal with a few specimens in which the sex characters were wanting in precision, and consequently a skull may possibly have been ascribed to the wrong sex. If we grant that this has occurred in a small minority, yet from the numerous specimens at my disposal, in which the sex could confidently be stated, the general conclusions cannot have been materially affected.

I propose, in the first instance, to analyse the dimensions, proportions, and form of the cranial box, and afterwards to consider those of the face.

The Cranial Box.

The shape of the cranium, from its influence on the form of the head and from its association with the brain contained in its cavity, has attracted attention from the earliest periods of craniological research. Since the time of Anders Retzius the relations of the length to the breadth and the grouping of skulls into those in which the cranium is relatively narrow and elongated, and those in which it is more rounded in form, have been regarded as of great importance in the recognition of racial distinctions. According to modern

[1] *Trans. Roy. Soc. Edin.*, vol. xl. part iii., 1903.

methods the character of the cranium can be determined by combining observations on its shape with exact measurements. The measurements are taken with callipers in straight lines between certain definite points, in order to determine the length, breadth, and height of the exterior of the box; with a graduated tape over the curved walls of the outer table so as to determine its arcs and circumferences, and with shot to estimate its internal capacity. The points of measurement in the straight lines are indicated by the terms employed in the Tables.[1] The measurements of the curved surfaces, whilst agreeing with the methods pursued in my memoirs in the *Challenger Reports*[2] and in my two memoirs on Indian crania[3] in regard to the horizontal circumference, the vertical transverse arc, and the frontal, parietal, occipital and total longitudinal arcs, have in this memoir been somewhat amplified so as to yield a vertical transverse circumference and a total longitudinal circumference, dimensions which for the first time are definitely stated in my Tables. The vertical transverse circumference is obtained by measuring with callipers a basal transverse diameter between opposite supra-auricular points, and adding this to the vertical transverse arc. The data for obtaining a total longitudinal circumference existed in the Tables in my previous memoirs, and consisted of the total longitudinal arc, the antero-posterior diameter of the foramen magnum, and the basi-nasal diameter; in this memoir the respective measurements have been added together and stated collectively in the Tables. The capacity of the cranial cavity has been taken by the method described in my *Challenger Report*, 1884, and the additional experience of its accuracy which I have had since that date has added to my confidence in the method as giving a close approximation to the real capacity, and not an exaggerated statement of the cubage, such as is obtained by the well-known method of PAUL BROCA.

Speaking generally, and subject of course to occasional exceptions, we may say that the Scottish cranium is large and capacious; the vertex is seldom keeled or roof-like, but has a low rounded arch in the vertical transverse plane at and behind the bregma, and with a gentle slope from the sagittal suture to the parietal eminences. The side walls are not vertical, and bulge slightly outwards in the parieto-squamous region, so that the greatest breadth is usually at or near the squamous suture. The occipital squama bulges behind the inion, and the slope from the obelion is downwards and backwards, so as to give in the *norma verticalis* an obliquely flattened character to the post-parietal region, but without occasioning a vertical parieto-occipital flattening such as is found in many normal brachycephalic crania, or in those in which artificial compression is employed in infancy. Owing to the width in the parieto-squamous region and the projecting occipital squama (probole) in many crania, their outline is more or less pentagonal, the frontal region forming one boundary, the sides of the cranium as far back as the parietal eminences forming two others, and

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[1] The Memoir contains seventeen Tables of measurements.
[2] *Zoology*, part xxix., 1884, and part xlvii., 1886.
[3] *Trans. Roy. Soc. Edin.*, part i., 1899; part ii., 1901.

the remaining two sides are the walls from the parietal eminences to the most projecting part of the occiput. In men the glabella and supraorbital ridges are fairly but not strongly pronounced, the forehead only slightly recedes from the vertical plane, and the nasion is scarcely depressed.

Length.—The glabello-occipital or maximum length was measured in one hundred and seventy-six crania, viz., one hundred and seventeen men and fifty-nine women. In the men the longest skull was 204 mm., and eight were 200 mm. and upwards; thirty-three were from 190 to 199 mm., so that nearly one-fourth of these crania were above 190 mm. in greatest length. The shortest skull in the men was 167 mm., and only sixteen crania were below 180 mm. in their greatest length. The longest skull in the women was 193 mm., and only three crania were 190 mm. and upwards; the shortest woman's skull was 161 mm.; and eight crania were below 170 mm. The mean length of the male crania was 186·6 mm., that of the female crania was 178·7 mm.

The projection of the glabella was not, even when most prominent, equal to what one sees in the long skulls of so many Australian and other black people, and consequently the length of the Scottish skull indicated a cranial cavity and a brain longer than existed in the dolichocephalic black races. Owing, however, to the depth of the frontal sinuses and the thickness of the frontal and occipital bones the cranial length from the glabella to the occipital point is appreciably greater, especially in the male sex, than the long diameter of the cerebrum. In order to eliminate the frontal sinus with the consequent projection of the glabella from the comparison, and to associate the length of the skull more closely with the length of the cranial cavity and the cerebrum, it was suggested by Dr ROLLESTON [1] that the point to be selected in front for taking the cranial length should be the ophryon, a point immediately above the glabella. The observations of A. LOGAN TURNER [2] have shown that the frontal sinus is not limited to the region of the glabella and supraorbital ridges, but extends in a large proportion of skulls above the ophryon, so that the influence of the sinus in adding to the cranial length is by no means eliminated by selecting the ophryo-occipital in preference to the glabello-occipital diameter. (Figs. 25, 26, pl. v. of the original Memoir.)

Breadth.—The greatest parieto-squamous breadth was obtained in one hundred and seventy-four crania, viz., one hundred and fourteen men and sixty women. In the men the broadest skull was 159 mm., and twenty-four crania were between 150 and 159 mm. The narrowest male skull was 130 mm., and twenty-six skulls ranged from 130 to 139 mm. In the women the broadest skull was 153 mm., two specimens being of that diameter. The narrowest skull was 128 mm., and thirty-six specimens ranged from 130 to 139 mm., whilst nineteen were between 140 and 150 mm. The mean breadth of the male crania was 149·3 mm., that of the female was 138 mm.

[1] In Greenwell's *British Barrows*, p. 506, 1877, and in vol. i. *Scientific Papers and Addresses*, edited by W. Turner.
[2] *Accessory Sinuses of the Nose*, p. 105. Edin., 1901.

This diameter approximates to the greatest breadth of the cerebrum in each individual.

In addition to the parieto-squamous breadth the Tables contain the minimum and stephanic breadth measurements of the frontal region, as well as the asterionic diameter which gives the breadth of the occipital bone between its lateral angles. As a general rule the frontal stephanic diameter materially exceeded the minimum frontal, though in a few instances it was not more than from 2 to 8 mm. greater. These dimensions give an approximation to the width of the frontal lobes of the cerebrum. Twenty-three crania had a persistent frontal suture, viz., sixteen males and seven females. The metopic crania as a rule exceeded in their frontal diameter the skulls of the corresponding sex from the same locality in which the frontal suture was ossified, and confirmed the view entertained by many craniologists that persistence of the frontal suture contributes to an increase in the transverse diameter of the skull and brain in that region.

The asterionic diameter, except in one skull, was greater than the minimum frontal, but as a rule it was less than the stephanic, though there were several exceptions. This diameter may be regarded as giving an indication of the breadth of the cerebellum.

Cephalic Index.—As is well known, this index expresses the relation which the greatest parieto-squamous breadth of a skull bears to its maximum length, the length being regarded as = 100, and the formula is as follows :

$$\frac{\text{greatest breadth} \times 100}{\text{maximum length}}.$$

The index was obtained in one hundred and seventy-four skulls, one hundred and fourteen of which were males and sixty were females. The index showed a great range of variation from 87·2 to 68·2. The mean length-breadth index in the men was 77·4, in the women 77·2. Both sexes, taken collectively, had essentially the same mean index, and were in the middle of the mesaticephalic group. If we follow the customary arbitrary grouping of crania according to the length-breadth or cephalic index, we find that forty-nine skulls were below 75, *i.e.* dolichocephalic; ninety skulls were between 75 and 79·9, *i.e.* mesaticephalic (mesocephalic); thirty-five skulls were 80 or upwards, *i.e.* brachycephalic.

Although it is a matter of convenience to accept a mesaticephalic group, interposed between the more extreme dolichocephalic and brachycephalic forms, it should be kept in mind, as I have stated in my memoir on Indian craniology,[1] that if we take 77·5 as marking a division of this group into two sections, the skulls which have an index between 77·5 and 80 approach in their characters more closely to the brachycephalic, whilst those that range from 77·5 to 75, on the other hand, are more allied to the dolichocephalic type. In these crania forty-five mesaticephali had their indices from 77·5 to 79·9, in no fewer than eighteen of which the index was between 79 and 80,

[1] *Trans. Roy. Soc. Edin.*, vol. xxxix. p. 744, 1899.

brachycephalic therefore in form, though they were fractionally below its lowest numerical limit.

It is obvious, therefore, that a strong brachycephalic strain pervades the population of Scotland at the present time, as in no fewer than fifty-three crania of this series the index was 79 or upwards, either numerically brachycephalic or closely approximating thereto. If expressed in percentages we may say that 20% were numerically brachycephalic and an additional 10% had a cephalic index from 79 to 79·9; on the other hand, 28% were dolichocephalic, and in 42% the index ranged from 75 to 79.

The relative proportion of the more rounded to the more elongated heads varied, however, materially in the different counties. Of the sixteen skulls from Fife six had the index above 80, one of which was hyperbrachycephalic, two were 79·7, three were between 77·5 and 79. In the Lothians, including Edinburgh and Leith, of seventy-nine skulls twenty had the length-breadth index 80 and upwards, and of these four were hyperbrachycephalic; eight crania also ranged from 79 to 79·9 and were thus essentially brachycephalic, whilst fourteen ranged from 77·5 to 78·9. In the group of nine skulls from Stirlingshire, Lanarkshire, Peebles, and Roxburghshire, two had a length-breadth index above 80, and one of these was hyperbrachycephalic, and three others were 78 or 78·1. The Renfrewshire group of twenty-one crania, on the other hand, had no specimen with an index as high as 80, though three were between 79 and 80, and three were from 77·5 to 79. The three skulls from Ayrshire had one brachycephalic example. Of the six skulls from the north-eastern counties of Forfar, Kincardine, and Banff, four had the length-breadth index 80 or upwards, and one of these was hyperbrachycephalic; the remaining two were 79·7 and 79·9 respectively, and were essentially brachycephalic. In the five crania from Shetland, one was hyperbrachycephalic, and another had the index 79·4. Of the five crania from Iona the two highest were 79 and 79·3 respectively. In the miscellaneous series of sixteen crania from the dissecting-room, only one had an index 80, no specimen was between 79 and 80, and four were from 77·5 to 79.

Our attention should now be directed to the distribution of dolichocephalic crania in the different counties; and along with those whose index is below 75, we shall consider the crania in the mesaticephalic group with an index between 75 and 77·4. In the Fifeshire group only three had the length-breadth index below 75, and two were 75·5 and 76 respectively. Of seventy-nine skulls from the Lothians twenty were below 75, and two of these were hyperdolichocephalic, while sixteen ranged from 75 to 77·4. Two crania from Lanark were below 75, and one of these was hyperdolichocephalic; two from Roxburgh were 76·2 and 76·3 respectively. In the Renfrewshire group eight skulls were dolichocephalic, and seven were between 75 and 76·7. Two of the three Ayrshire skulls were 75 and 75·9 respectively. Two of the four Wigtownshire were dolichocephalic, the other two were 75·8 and 76·5 respectively. No skull from Shetland was below 75, but three were from 75·1 to 77·4. In three crania from Caithness and six from the Highland counties of Argyll, Perth, Ross and

Sutherland, the length-breadth index was in no instance above 75, and two of these were hyperdolichocephalic. Five of the seven crania from the Hebrides ranged from 74·2 to 77. Seven of the dissecting-room series were below 75, and four ranged from 75·7 to 77·1.

From this analysis of the cephalic indices in the crania under observation it would appear that a brachycephalic type of skull prevailed in Fife, in the Lothians, in the north-east counties of Forfar, Kincardine, and Banff; and it occurred to some extent in Shetland, in Ayr, in the border county of Peebles, and in Stirlingshire.

The dolichocephalic type of skull was feebly represented in Fife; it was proportionately more numerous in the Lothians, in which district are included the skulls from Edinburgh and Leith; it was represented in Lanark, Ayr, Shetland, and the Hebrides. It formed the prevailing type in Wigtownshire, in Caithness, in the skulls from the High' :nd counties, and in the important series of skulls from Renfrew ...ire. Whilst examples of this type occurred generally throughout the series, it , may be noted that only five hyper-dolichocephali, *i.e.* skulls with the index below 70, were measured, but that eght hyper-brachycephalic crania, *i.e.* with the index 85 and upwards, occurred in the series.

In the study of the Scottish brachycephalic crania I have been led to compse them with crania of some other races measured by me some years ago, which had numerically this type of head. The comparison has been made with twenty-four male Burmese skulls [1] and with eight skulls of male Sandwich Islanders [2] described in previous memoirs, in each of which the cephalic index was 80 or upwards. The mean length-breadth index in the Burmese brachy-cephali was 84·2. The shortest skull in this group was 158 mm., the longest was 184, and the mean length was 171·8 mm. The parieto-squamous breadth ranged from 139 to 153 mm., and the mean breadth was 144·7 mm. In the Sandwich Islands brachycephali the mean length-breadth index was 83·8 ; the length ranged from 169 to 184 mm., and the mean was 176·5 mm. ; the breadth ranged from 142 to 155 mm., and the mean was 148 mm. In twenty seven male brachycephalic Scottish skulls the mean length-breadth index was 83·2, almost the same as that of the Burmese. The length ranged from 167 to 193 mm., and the mean was 180·3 mm. ; the breadth ranged from 140 to 159 mm., and the mean was 150 mm. The mean length of the Scottish brachycephalic crania exceeded, therefore, by several millimetres the length of the brachycephalic Burmese and Sandwich Islanders. The greater length in the Scottish brachycephali was associated with a backward projection of the occipital squama, which contrasted with the almost vertical post-parieto-occipital region in the Burmese, Siamese, and brachycephalic Sandwich Islanders. For the production of a high index in skulls of this type, the breadth

[1] See my Memoir on Indian Crania, part i., *Trans. Roy. Soc. Edin.*, vol. xxxix., 1899.
[2] See *Challenger Report*, "Zoology," part xxix., 1884, pp. 64 and 66, and part xlvii., 1886, p. 125.

required to be proportionately increased, and the Scottish brachy-cephalic crania both in length and breadth were larger and more capacious than the brachycephalic Burmese and Sandwich Islanders.

Height.—The distance from the basion to the bregma was taken as expressing the height of the cranium, and it was measured in one hundred and fifty specimens, ninety-eight of which were males and fifty-two females. In the men the highest skull was 145 mm.; fifteen skulls were between 140 and 145, fifty between 130 and 140, and thirty-four below 130, the lowest being only 117 mm. in height. The mean height of the male skulls was 132·4 mm. In the women the highest skull was 140 mm., the lowest was 118 mm., and the mean was 126. If we compare the height of the male Scottish crania with that of the male Burmese already referred to, we find that the mean height in the latter people was 135 mm., a somewhat greater figure than in the Scottish specimens.

Vertical Index.—This index expresses the relation which the basi-bregmatic height bears to the maximum length, which is regarded as = 100, and is computed by the formula

$$\frac{\text{basi-bregmatic height} \times 100}{\text{maximum length}}.$$

The index was obtained in one hundred and fifty crania, ninety-eight of which were men and fifty-two women. It was subject to a great range of variation, from 63·7 to 79·4. The mean vertical index in the men was 70·9, in the women 70·5; both were metriocephalic,[1] and the sexual difference was very slight, though slightly in favour of the men. The number of skulls with vertical index 75 and upwards was seventeen; thus a small proportion only were hypsicephalic or high skulls; sixty-five crania on the other hand had the vertical index below 70, *i.e.* were low skulls, chamæcephalic or tapeinocephalic; the remainder had the index between 70 and 75 and were metriocephalic, which, as above stated, was the mean of the entire series.

Breadth-Height Index.—The relations of the length to the breadth and to the height of the cranium have long been recognised as important subjects of investigation in the study of the racial characters of skulls, but the relations of the breadth and height to each other have not had an equal attention given to them.

In my *Challenger Report* (1844) I pointed out that in the brachycephalic crania from New Guinea and other Pacific Islands, the breadth was as a rule greater than the height, whilst in the dolichocephalic Papuans the opposite condition prevailed. In subsequent memoirs, more especially those on Indian craniology, I called attention to the relations of these diameters in several Asiatic

[1] I prefer, for the reasons stated in my *Challenger Report*, 1884, to employ the descriptive term metriocephalic rather than orthocephalic, as recommended by the German craniologists in the Frankfurt agreement (*Archiv für Anthropologie*, Bd. xv. p. 1, 1884). In this memoir I have, however, adopted the numerical subdivision of the group which they have suggested, viz., chamæcephalic up to 70; metriocephalic (orthocephalic), 70·1–75; hypsicephalic, 75·1 and upwards.

races. In his work on the accessory sinuses of the nose already quoted, A. LOGAN TURNER has recorded the proportion of breadth to height in a large number of crania, European and exotic.

In order to express numerically the relations of the breadth and height of the cranium to each other, an index may be computed by the following formula :

$$\frac{\text{basi-bregmatic height} \times 100}{\text{parieto-squamous breadth}},$$

the breadth being regarded as 100. The data for obtaining the index exists in the Tables.

When the index exceeds 100, the height is greater than the breadth, and the skull is *hypsistenocephalic*,[1] *i.e.* a high narrow skull : when the index is less than 100, the breadth is greater than the height and the skull is *platychamæcephalic, i.e.* a wide low skull.

From the measurements which I have made of the breadth and height of the cranium in many races of men, I have ascertained that in some the height usually exceeded the breadth, whilst in others the breadth exceeded the height.[2] In well-pronounced dolichocephalic races like the Esquimaux, the Melanesians, the Dravidians, Veddahs, and the Australians generally, as a rule the height was greater than the breadth, and the crania were hypsistenocephalic. In the brachy-cephalic crania of the Burmese, Siamese, Chinese, Andaman Islanders, and brown Polynesians, on the other hand, the breadth as a rule was greater than the height and the crania were platy-chamæcephalic.

In the series of one hundred and fifty Scottish crania in which both the breadth and height were measured, in only two skulls was the height greater than the breadth, and in four others they were equal. In all the rest, whether the cephalic index was high or low, the vertical diameter was less than the breadth. A striking feature of the Scottish crania, therefore, was the preponderance of the cephalic index over the vertical index, notwithstanding the consider-able number of dolichocephalic skulls in the series, and in this respect the crania favoured the brachycephalic rather than the dolichocephalic type. The Scottish skulls are platychamæcephalic.

Horizontal Circumference.—This measurement was taken in one hundred and sixty-three skulls, one hundred and eight of which were males and fifty-five females. The maximum male skull was 572 mm., the minimum was 490 mm., and the mean was 531 mm. The maximum female skull was 550 mm., the minimum was 470 mm., and the mean was 506 mm.

[1] Dr BARNARD DAVIS introduced the term hypsistenocephalic to designate the high, narrow dolichocephalic crania of natives of islands in the Western Pacific (*Natuurkundige Verhandelingen*, Deel. xxiv., Haarlem, 1886), and I propose that it should have a more general application, as in the text. The term platy-chamæcephalic is now suggested to designate wide and low crania.

[2] See my Memoir in *Challenger Report*, 1884 ; also on New Guinea Skulls in *Proc. Roy. Soc. Edin.*, July 1899, and on Indian Crania in *Trans. Roy. Soc. Edin.*, 1899 and 1901.

Vertical Transverse Circumference.—This measurement was made in one hundred and fifty-three skulls, of which one hundred and three were males and fifty were females. The maximum male skull was 464 mm., the minimum was 398 mm., and the mean was 434 mm. The maximum female skull was 459 mm., the minimum was 381 mm., and the mean was 409·6 mm.

Total Longitudinal Circumference.—This dimension was taken in one hundred and thirty-nine crania, of which ninety-six were males and forty-three were females. The maximum male skull was 559 mm., the minimum was 468 mm., and the mean was 515·2 mm. The maximum female skull was 533 mm., the minimum was 441 mm., and the mean was 488·8 mm. The high longitudinal circumference was found in those skulls in which the glabello-occipital length was 200 mm. or approaching thereto, whilst in the skulls in which this diameter was small the longitudinal circumference was relatively low.

The total longitudinal arc was much the most important factor in this measurement, and the skulls were sufficiently numerous to enable me to ascertain the relative lengths of the frontal, parietal and occipital arcs which collectively form the total longitudinal arc in the series of skulls in which the arcs were measured; it was found that the occipital arc in thirteen specimens was greater than the frontal and in one hundred and thirty-one it was less; in twenty-six it was greater than the parietal and in one hundred and twelve it was less. It is the rule, therefore, for the frontal and parietal longitudinal arcs to exceed the occipital, though exceptions to the rule occur in recognisable numbers. The relative arcs of the frontal and parietal bones were measured in one hundred and fifty-eight crania; in ninety-six the frontal arc was longer than the parietal, in fifty-five the parietal was longer than the frontal, and in seven they were equal. It is obvious, therefore, that as so much variation occurs in the relative length of the longitudinal arcs in the three bones, they have no appreciable value as race characters in the Scottish skulls, and the variation occurred in both the brachycephalic and dolichocephalic types. The longest occipital arc was 139 mm., the shortest 94 mm.; the longest frontal arc was 148 mm., the shortest 111 mm.; the longest parietal arc was 148 mm., the shortest 102 mm.

From a comparison of the three circumferential measurements it will be seen that the horizontal circumference is the greatest, for it includes both the glabello-occipital and parieto-squamous diameters, which are the longest diameters in the Scottish crania. The vertical transverse circumference, again, is the shortest, as the basi-bregmatic diameter is the shortest of the three dimensions in the Scottish crania. The total longitudinal circumference ranks intermediate, for it includes only one of the two longer diameters.

Cubic Capacity.—The internal capacity of the cranium was taken with shot in accordance with the method which I described in 1884.[1] One hundred and fifteen crania were cubed; seventy-three were

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[1] *Challenger Reports*, "Zoology," part xxix., 1884.

males and forty-two were females. The maximum capacity in the male skulls was 1855 c.c., the minimum was 1230 c.c., and the mean was 1478 c.c. Thirty-three skulls were more than 1500 c.c., and of these seven were 1700 and upwards, nine were between 1600 and 1700, seventeen were between 1500 and 1600; further, twenty-two were between 1400 and 1500, sixteen were between 1300 and 1400, and four were below 1300 c.c. The maximum capacity in the female was 1625 c.c., the minimum was 1100, and the mean was 1322 c.c. Only three female skulls were above 1500 c.c., eight were between 1400 and 1500, sixteen were between 1300 and 1400, eighteen were below 1300, and of these six were below 1200 c.c. The general result approximates to what has been observed in the crania of other races and peoples, that the female skull is about 10 per cent. less capacious than the male. If I had employed BROCA's method, by which the cubic contents of so many races have been taken by anthropologists in France and elsewhere, the average for both sexes would have been considerably higher. It is possible, however, from the Tables compiled by E. SCHMIDT,[1] to state the cubic contents of the Scottish crania approximately in the terms of BROCA's method, according to which the mean capacity of the males would have been about 1570 c.c. and that of the females about 1400 c.c. The Scottish male skull therefore is, according to BROCA's method of cubage, somewhat in excess of the mean 1500 c.c. ascribed to the crania of European men.

In twenty-five dolichocephalic crania the mean capacity was 1516 c.c., and in twenty-one crania approximating to the dolichocephali in which the cephalic index was from 75 to 77·4 the mean capacity was 1519 c.c. In thirteen brachycephalic skulls the mean capacity was 1469 c.c., and in fifteen, in which the cephalic index ranged from 77·5 to 79·9, the mean capacity was 1452 c.c. A claim has been made by people whose crania have brachycephalic proportions that a brachycephalic head is higher in its type than a dolichocephalic. So far as the quality of type is expressed by the amount of cranial capacity, the skulls of the people of Scotland do not sustain this claim, as those with dolichocephalic proportions had a distinctly greater mean capacity than the brachycephali.

In addition to these more general statements, the Tables enable us to form some estimate of the existence of differences in the capacity of skulls from various districts of Scotland, though in many localities the number measured was too small on which to generalise. In the male skulls from Fife, Mid-Lothian, Shetland and Renfrewshire, the average in each group was, according to my measurements, somewhat more than 1500 c.c.; in East Lothian and Wigtownshire it was slightly lower than 1500; in the skulls from Edinburgh and Leith, West Lothian, the North-Eastern Counties, the Highland Counties and the Dissecting-room, the mean again was still lower. In making this statement I do not draw any inference that the difference in cranial capacity had a definite relation to the intellectual endowment of the people in these localities. Many other factors than the volume of the

[1] *Archiv für Anthropologie,* supplement, vol. xiii. p. 53, 1882.

cranial cavity have to be taken into consideration in the estimation
of the intellectual power either of individuals, or of a collection of
individuals belonging to the same people or race.

In the comparison of different races with each other there is, how-
ever, evidence that those in which the mean cranial capacity is low
are intellectually inferior to the races whose mean capacity is on a
distinctly higher scale.

If we take as an example the aboriginal Australians who are
recognised as a race incapable, apparently, of intellectual improvement
beyond their present condition, my measurements have shown that in
thirty-nine men the mean cranial capacity was 1280 c.c., whilst
twenty-four women were only 1156 c.c. Of the men, eight had a
smaller capacity than 1200 c.c., and four only were above 1400 c.c.;
whilst in the women ten were below 1100, and only three were 1200
c.c. and upwards.

The differences between the capacities of the native Australians
and the Scottish skulls are much more than can be accounted for by
variations in the stature and muscularity of the two peoples, and
undoubtedly express a size and quality of brain associated with
differences in the intelligence and the mental capabilities of the two
races.

The Face.

All craniologists from the time of PRICHARD and RETZIUS have
agreed in stating that in the study of the face it is important to
determine the degree of forward projection of the upper jaw and to
decide if the face is orthognathic or prognathic.

Gnathic Index.— In this memoir I have adopted the method
followed by Sir WM. H. FLOWER and compared the length from basion
to nasion with that from basion to the alveolar point. The basi-nasal
length was taken in one hundred and forty-nine skulls, and ranged
in the males from 91 mm. to 110 mm., and the mean was 101·4 mm.;
whilst in the females it ranged from 86 to 105, with a mean of 95·3
mm. The basi-alveolar length ranged in sixty-seven males from 81
mm. to 108 mm., and the mean was 96 mm.; whilst in thirty-one
females it ranged from 79 to 102, with a mean of 91 mm.

The gnathic index was computed as follows:

$$\frac{\text{basi-alveolar length} \times 100}{\text{basi-nasal length}}.$$

Whilst the index gives the numerical relation between the two
diameters, it does not necessarily express the relative projection of
the upper jaw beyond the profile outline of the face, for in many
skulls the nasion is depressed below the plane of the glabella and of
the forehead generally.

The gnathic index was computed in ninety-seven skulls, sixty-six of
which were men and thirty-one women. It ranged from 85·1 to
103·2, and the mean in the men was 94·5, in the women 94·8. If we
take FLOWER's subdivision of the group, and regard an index 103 as
marking the lowest limit of prognathism, only one specimen came

into that category. If an index 98 be taken as marking the upper limit of orthognathism, seventy-two skulls belonged to this group, whilst twenty-four had indices from 98 to 103 and were mesognathous. The Scottish skulls are therefore characterised by an almost complete absence of prognathism.

It is sometimes stated that in the same race or people the women show a relatively greater prognathic character than the men. This can scarcely be said of the Scottish skulls, for the difference between the two sexes was only fractional, so that for all practical purposes they may be regarded as identical.

Orbital Index.—BROCA paid much attention to the determination of the height and width of the orbit and to the computation of an index of their relative proportions. The width was measured from the dacryon, or point of junction of the frontal, lachrymal and ascending process of the maxilla, to the most distant point on the edge of the outer border of the orbit. These measurements were taken in one hundred and twenty-four skulls. The greatest width in eighty-four males was 46 mm., the least was 35 mm., and the mean was 39 mm.; in forty females the greatest width was 41 mm., the least was 35, and the mean was 37·4 mm. The greatest height in the males was 41 mm., the least was 28 mm., and the mean was 34 mm.; in the females the greatest height was 37 mm., the least was 29 mm., and the mean was 33 mm.

The orbital index is obtained as follows :

$$\frac{\text{orbital height} \times 100}{\text{orbital width}}.$$

The index was computed in one hundred and twenty-five skulls, of which eighty-four were men and forty-one were women. It ranged from 73·7 to 105·1, and the mean was 86·4.

In grouping skulls in their orbital and nasal indices I have in this, as in my previous craniological memoirs, adopted the terms employed by BROCA and FLOWER, as well as their numerical divisions of the groups. An orbit is said to be microseme when the height is low in relation to the width and the index is below 84. Thirty-three skulls came into this group. On the other hand, when the height and width closely approximate so that the base is rounded and the index is 89 and upwards, the orbit is megaseme, and to this group fifty-seven specimens belonged, and in three of these the index was 100 or upwards. Orbits are named mesoseme when the index is between 84 and 89, and thirty-three skulls fell into this category. In Scottish skulls the rule was for the orbit to be high in relation to the width, and somewhat rounded in outline, though exceptions not unfrequently occurred. My observations on the orbital index in the skulls of numerous races have satisfied me that it presents a great range of variation in the same race, and that it possesses only a secondary value as a race character.

Nasal Index.— The relation between the height of the nose, measured from the nasion to the lower border of the apertura pyriformis, and the greatest width of that aperture, constitutes one of

the most important anthropological characters of the face. In eighty-four male skulls the height ranged from 60 mm. to 46 mm., and the mean was 53·5 mm.; in thirty-eight females the range was from 57 mm. to 44 mm., and the mean was 49·9 mm. In eighty-two males the nasal width ranged from 28 mm. to 19 mm., and the mean was 23·1 mm. In thirty-five females the range was from 26 mm. to 19 mm. with a mean of 22·1 mm. The nasal index expresses the numerical relation between the width and height, and is computed as follows, the height being $= 100$:

$$\frac{\text{nasal width} \times 100}{\text{nasal height}}.$$

The index was obtained in one hundred and twenty-three specimens, eighty-one males and forty-two females. It ranged from 55·3 to 34·5; the mean was 42·5, and with few exceptions the height was more than twice the width. If with BROCA and FLOWER we regard all skulls in which the nasal index is 53 and upwards as platyrhine, i.e. with the pyriform aperture wide in relation to the height of the nose, only four specimens exhibited this character. On the other hand, in ninety-three skulls the anterior nares were narrow and elongated, and the nasal index below 48 was leptorhine, and in fourteen of these specimens the index was below 40. The remaining twenty-six skulls had the index ranging from 48 to 53 and formed an intermediate or mesorhine group. The occurrence of wide nostrils in the Scottish face may be regarded therefore as accidental, and due perhaps to intermixture, through an ancestor, of a strain of some race in which a platyrhine nose was an ethnic character. The four platyrhine specimens were one in each of the East-Lothian, Mid-Lothian, Highland and Dissecting-room groups. The customary form of nose in Scotland is long, relatively narrow, with a well-marked bridge, and projecting so that the type of face is prosopic, which means that the nose distinctly projects beyond a line drawn between the anterior part of the two malar bones.

Facial Indices.—An important character which has been systematically studied by KOLLMANN is the relation between the length and breadth of the face in different crania.[1] The length or height of the entire face is measured from the nasion to the lower border of the symphysis menti, whilst the breadth is between the most projecting parts of the two zygomata. In twenty-one male skulls measured, the longest face was 137 mm., the shortest was 104 mm., and the mean was 120·7 mm.; in six females, the mean length was 108·8. In sixty-eight male skulls the greatest breadth was 144 mm., the least was 117 mm., and the mean was 132·2 mm. In thirty female skulls the greatest breadth was 135 mm., the least was 115 mm., and the mean was 121·5 mm. With one exception, in which the length and breadth were equal, the breadth of the face exceeded the length.

[1] Rassen Anatomie der europäischen Menschenschädel in *Verhandl. der Naturforschenden Gesellschaft* in Basel, viii. Theil, 1 Heft. 1886.

A *complete or nasio-mental facial index* can be computed as follows :

$$\frac{\text{nasio-mental length} \times 100}{\text{interzygomatic breadth}}.$$

As so frequently happens in craniological collections, the lower jaw had been preserved in only a small number of the skulls, and the complete facial index could only be taken in twenty-six specimens, twenty-one males and five females; the mean of the series was 90 : that of the males was 92·3, that of the females 87·8.

KOLLMANN divides skulls and heads into two groups according to the relation of the length to the breadth of the face. When the index is 90·1 or upwards the face, he says, is leptoprosopic, high (long) or narrow faced ; when the index is below 90·1 it is chamæprosopic, low or broad faced. In the study of the proportions of the face, and in grouping skulls in accordance with their facial indices, it is useful, as in the other relative proportions of the skull, to have a group intermediate between the two more extreme forms. We may appropriately speak, therefore, of a third or mesoprosopic group, and include in it those skulls and heads in which the index ranges from 85 to 90, both inclusive. The chamæprosopic group under this arrangement would consequently be limited to those heads in which the index is below 85. In the series of Scottish crania under consideration eighteen were leptoprosopic, four were mesoprosopic, and only four were chamæprosopic in my more limited use of the term.

To obtain as far as possible an idea of the relation between the length and breadth of the face in skulls where the lower jaw is absent, KOLLMANN has suggested that the interzygomatic breadth should be compared with the length of the superior maxilla measured from the nasion to the alveolar point between the two central incisors. Seventy-nine crania were measured in these diameters, viz., fifty-six males and twenty-three females.

The male crania ranged in the maxillary length from 61 mm. to 84, and the mean was 71·6 mm. The female crania ranged from 60 to 74 mm., and the mean was 67 mm. An index, which may be appropriately named *maxillo-facial*, can be computed as follows :

$$\frac{\text{nasio-alveolar length} \times 100}{\text{interzygomatic breadth}}.$$

The maxillo-facial index was taken in seventy-nine skulls, fifty-five of which were males and twenty-four females. It ranged from 61·8 to 46·5, and the mean was 54·6.

In grouping crania under the maxillo-facial index, KOLLMANN employs the same terms, leptoprosopic and chamæprosopic, as in the divisions of the complete facial index, but the numerical limits of the two groups, owing to the length representing only a segment of the complete face, are necessarily different. When the maxillo-facial index is 50·1 and upwards, he regards it as leptoprosopic ; when 50 or less, it is chamæprosopic. In this memoir I have retained the numerical limit of the leptoprosopic group, and find that with seven

exceptions all the skulls belonged to it, and that in five leptoprospic specimens the index ranged from 60·3 to 61·8. If a division of the chamæprosopic group of KOLLMANN into mesoprosopic and chamæprosopic were adopted for the maxillo-facial as I have suggested for the complete facial index, and 45 were taken as the lower numerical limit of the mesoprosopic group, the seven exceptional skulls above referred to would fall into that group. No skull, therefore, in its maxillo-facial index was chamæprosopic in this more restricted use of that term, and the general type of the face in the Scottish crania is leptoprosopic.

The facial indices may be grouped as follows :

	Complete facial.[1]	Maxillo-facial.
Leptoprosopic, .	. 90·1 and upwards, .	. 50·1 and upwards.
Mesoprosopic, .	. 85 to 90, . . .	. 45 to 50.
Chamæprosopic, .	. below 85, . .	. below 45.

A low or chamæprosopic maxillo-facial index necessarily depends on the upper jaw being short, in relation to the breadth of the face, and to produce a chamæprosopic complete facial index in both the upper and lower jaws being relatively short. A relatively short upper jaw necessarily also affects both the height of the nose and the height of the orbit, so that one would expect to find a chamæprosopic face associated with a low and possibly a platyrhine nose and with a low or microseme orbit. The Scottish face is therefore long and narrow in comparison with the broad, squat faces in the Mongolian and some other types of head. In the Esquimaux, for example, the mean interzygomatic diameter in eighteen males was 138·0 mm., whilst in the Scotsmen it was only 132·2 mm.

Palato-alveolar or Palato-maxillary Index.—Anthropologists concur in considering that the relations between the length and breadth of the hard palate in the races of men should be enquired into. BROCA[2] and VIRCHOW[3] limited the measurements in this region to the hard palate itself, and computed an index which has been named staphylin or palatal. FLOWER[4] modified and improved these measurements by including the alveolar arch, and computed an index which he termed maxillary. In my *Challenger Report*[5] I suggested that the terms palato-maxillary or palato-alveolar were to be preferred, as expressing more fully the parts measured and the index which is computed from them. The length is taken from the alveolar point to the midpoint of a line drawn between the hinder ends of the alveolar borders, and the width is between the outer part of the alveolar arch opposite the second upper molar tooth. The palato-alveolar

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[1] The complete or nasio-mental facial index corresponds, in the diameters from which the index is computed, with the zygomatic facial index of KOLLMANN. The maxillo-facial index corresponds with the upper facial index of KOLLMANN in the points of measurements.

[2] *Instructions craniologiques*, p. 77.

[3] *Archiv für Anthropologie*, Bd. xv. s. 5, 1884.

[4] "Cranial Characters of Fiji Islanders," *Journ. Anthrop. Inst.*, November 1880.

[5] 1884, p. 7, and *Journ. Anat. and Phys.*, vol. xvi. p. 185, October 1881.

length in fifty-five males ranged from 46 to 62 mm., and the mean was 55·6 mm.; in twenty-eight females the range was from 45 to 59 mm., with a mean 51 mm. The palato-alveolar breadth in the males ranged from 50 to 71 mm., and the mean was 60·9; in the females the range was from 52 to 64 mm., with a mean of 58·3 mm.

The palato-alveolar index was computed as follows:

$$\frac{\text{palato-alveolar breadth} \times 100}{\text{palato-alveolar length}}.$$

In my *Challenger Report* I suggested that relatively long palato-alveolar regions with an index below 110 should be named dolichuranic; relatively wide palates with an index above 115, brachyuranic; and those with an intermediate index between 110 and 115, mesuranic. As skulls exhibit, however, a wide range in the index in this region, I now make the further suggestion that when the index falls below 105 it should be called hyperdolichuranic; where it exceeds 120, hyperbrachyuranic. The divisions of the group may be expressed in tabular form as follows:

Hyperdolichuranic, ...	below 105.
Dolichuranic, ...	105 to 110.
Mesuranic, ...	110 to 115.
Brachyuranic, ...	115 to 120.
Hyperbrachyuranic, ...	above 120.

In this series of Scottish skulls nineteen were hyperbrachyuranic; seventeen were brachyuranic; fifteen were mesuranic; twenty were dolichuranic; and eleven were hyperdolichuranic. In only three specimens, two females and a male, was the length greater than the breadth; but in twenty-eight skulls the length was considerable in relation to the breadth, though not greater, so that the palate had an elongated appearance. As a rule, however, the breadth of the region was materially greater than the length, and the form of the palato-alveolar arch was that of a wide horseshoe.

Lower Jaw.—This bone had been preserved in only thirty-five skulls, twenty-six of which were males. In several of these, many teeth had been lost during life and their alveoli absorbed, so that the form of the bone had been more or less modified. Where the teeth had been in great part preserved, the body of the jaw had in the male sex a vertical diameter at the symphysis, ranging from 26 to 37 mm., and with a well-defined chin; the ascending ramus was broad and the angle was pronounced. The entire jaw had in most specimens a massive appearance, which had materially contributed to give character to the face, and from the marked vertical diameter of the body of the bone had constituted an important factor in giving to the entire face a length which placed it distinctly in the leptoprosopic group. The condyloid and coronoid diameters of the jaws varied in relative length in the series: in seventeen specimens the height from the angle to the top of the condyl was greater than to the tip of the coronoid, whilst in thirteen the coronoid height was longer, and in three specimens they were equal. The intergonial width ranged in the male jaws from 88 to 114 mm., and the mean of twenty-four

specimens was 100 mm., a diameter between the angles of the jaw materially below the interzygomatic, intermalar and stephanic breadths, but distinctly higher than the minimum frontal diameter.

To assist the reader in obtaining a bird's-eye view of the dimensions and proportions of the constituent parts of the Scottish skulls studied in this memoir, I have prepared Table XVI., in which I have stated for both sexes the maximum and minimum dimensions, as well as the mean of the principal measurements in the series of skulls, together with the maximum, minimum and mean of the the respective indices. I have also, by way of comparison, included in the Table the mean diameters and indices of a number of skulls of male aboriginal Australians which I have measured.

TABLE XVI.

	Scottish Skulls						Australians
	Females.			Males.			Males.
	Max.	Min.	Mean.	Max.	Min.	Mean.	Mean.
Cubic capacity, . . .	1625	1100	1322	1855	1230	1478	1280
Glabello-occipital length, . .	198	161	178·7	204	167	186·6	191·3
Basi-bregmatic height, .	140	118	126	145	117	132·4	135
Vertical index, . . .	*77·6*	*64·*	*70·5*	*79·4*	*63·7*	*70·9*	*70·6*
Greatest parieto-squamous breadth, . . .	153	128	138	159	130	149·3	132
Cephalic index, . . .	*87·9*	*69·3*	*77·2*	*87·2*	*68·2*	*77·4*	*69·*
Horizontal circumference, .	550	470	506	572	490	531	530
Vertical transverse circumference, . . .	459	381	409·6	464	398	434	...
Basi-nasal length, . .	105	86	95·3	110	91	101·4	...
Basi-alveolar length, . .	102	79	91	108	81	96	...
Gnathic index, . . .	*100·*	*86·7*	*94·8*	*103·2*	*83·*	*94·5*	*100·6*
Total longitudinal circumference, . . .	537	441	488·8	559	468	513·2	...
Interzygomatic breadth, . .	135	115	121·5	144	117	132·2	...
Nasio-mental length, .	114	102	108·8	137	104	120·7	...
Complete facial index, .	*92·2*	*82·5*	*87·8*	*100·*	*79·3*	*92·3*	...
Nasio-alveolar length, .	74	60	67	84	61	71·6	...
Maxillo-facial index, . .	*61·8*	*48·*	*55·1*	*60·8*	*46·5*	*54·3*	...
Nasal height, . . .	57	44	49·9	60	46	53·5	...
Nasal width, . . .	26	19	22·1	28	19	23·1	...
Nasal index, . . .	*54·*	*34·5*	*44·4*	*55·3*	*37·9*	*38·9*	*57·*
Orbital width, . . .	41	35	37·4	46	35	39	...
Orbital height, . . .	37	29	33	41	28	34	...
Orbital index, . . .	*102·8*	*73·7*	*84·6*	*105·1*	*76·9*	*87·2*	*81·3*
Palato-alveolar length, .	59	45	51	62	46	55·6	...
Palato-alveolar breadth, .	64	52	58·3	71	50	60·9	...
Palato-alveolar index, .	*130·6*	*94·5*	*109·8*	*130·*	*98·2*	*113·*	*109·*

INDEX.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

JULY 1902.

THE Summer Meeting of the Anatomical Society of Great Britain
and Ireland was held in the Medical School of St Bartholomew's
Hospital, E.C., on Thursday the 3rd and Friday the 4th of July 1902.
The President, Mr C. B. LOCKWOOD, occupied the chair. On
Thursday the meeting commenced at 3 P.M. and lasted until 5.15 P.M.;
twenty-seven members and four visitors were present. On Friday
the meeting commenced at 3 P.M. and lasted until 5.30 P.M.; twenty-
four members and two visitors were present. Letters regretting
inability to attend were received from Prof. A. H. YOUNG, Prof.
MUSGROVE, Dr BRYCE, and others.

The minutes of the last meeting were read and confirmed.

The following communications were made :—

(1) Dr R. J. A. BERRY showed two cases of *twin monsters* (females),
both of which had occurred in the practice of Dr F. W. N. HAULTAIN,
Edinburgh.

1. In the first case the twins were full term and well developed.
The line of fusion was along the anterior abdominal wall, from the
ensiform process to rather below the umbilicus. Subsequent dis-
section showed the twins to be normal in every respect with the
following exceptions :—

(a) The two stomachs are united by a single duodenal tube, from
the centre of which proceeds a single jejunum common to both twins;
this single jejunum subsequently divides into an ileum for each twin,
the large intestine of each of which is perfectly normal.

(b) There is a single liver, placed astride the single duodenum in
such a way as to appear as though it were bifurcated. The gall-
bladder is absent.

(c) There is a single pancreas common to both twins, and only one
spleen.

2. In the second case the line of fusion is more extensive, including
the thoracic wall as well as the abdominal wall. The left upper limb
of the right twin is fused with the right upper limb of the left twin,

h

with the exceptions of the two hands of these limbs which remain separate. The following peculiarities are present:—

(a) The alimentary canal is precisely similar to that of the first case, but a Meckel's diverticulum is present.

(b) The liver resembles that of the first case, but a gall-bladder is present.

(c) There is only one pancreas and one spleen, as in the first case.

(d) There is a single heart, giving off a right-sided aorta for the right twin and a left aorta for the left twin.

(e) The inferior venæ cavæ of the two twins fuse together in the substance of the single liver to form a single vessel which opens into the single right auricle.

(f) There are two superior venæ cavæ, which open into the single auricle.

(2) *Flexor Carpi Radialis of Elephant, shewing great development of elastic tissue.* By Mr R. H. BURNE, B.A.

This specimen, exhibited by the kind permission of Professor STEWART, is a transverse section through the flexor carpi radialis of an Indian elephant. The muscle tissue has been partly dissected away to show in relief a strong development of elastic tissue in the perimysium.

This tissue forms a thick layer upon the exposed surface of the muscle, connected with elastic bands and sheets of various sizes running between the muscle bundles.

Towards the distal end of the muscle these elastic bands converge towards the superficial sheet, and the latter, suddenly assuming a tendinous character, becomes the proximal part of the tendon of insertion of the muscle.

A similar but less marked development of elastic tissue between the muscle bundles was observed in another fore-limb muscle (probably the flexor profundus), but the beast was fleshed before we saw it.

The flexor carpi radialis of the elephant is described by Miall and Greenwood in the *Journal of Anatomy* for 1878, and this development of elastic tissue noticed.

They speak of the muscle as formed of "alternate layers of muscle and elastic tissue in about equal proportions"—a description not strictly applicable to this specimen.

With regard to the probable use of this elastic muscle to the creature, Miall and Greenwood make the following remarks:—

"This . . . . peculiarity would give rigidity to the limb when extended in a perfectly straight line. When the animal stands the toes are over-extended so that the flexor carpi radialis, stretched *like the chord across an arc,* tends to draw the carpus upwards and forwards, and opposes the flexors. When, on the other hand, flexion has carried the limb beyond the neutral line, the elastic band assists the flexors, drawing the carpus upwards and backwards."

From the position of the muscle in the limb, and its insertion upon the

Elastic tissue
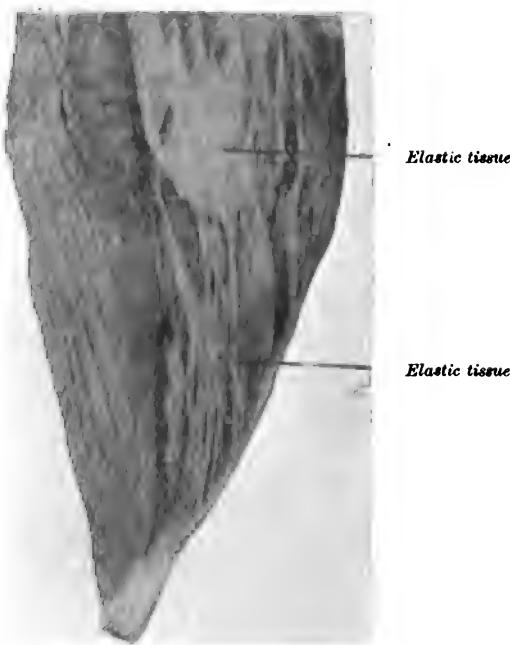
Elastic tissue

FIG. 1.—Distal end of flexor carpi radialis of the Indian elephant, seen from the deep aspect ; muscle bundles partly dissected away on right side to show elastic tissue.
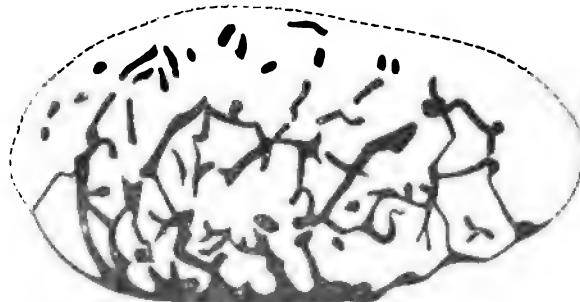
FIG. 2.*—Diagram of transverse section through upper part of flexor carpi radialis of *Elephas indicus* ; elastic tissue black.

posterior surface of the carpus, it does not seem that such an action in *aid* of extension, as suggested by Miall and Greenwood, could possibly occur.

* From a block kindly lent by the Royal College of Surgeons of England.

Rather one would suppose that this tissue would tend to passively *prevent* over-extension when standing, and perhaps even more would obviate risk of rupture of the muscle under the severe strain put upon it when, in running, the flexor muscles have the vast weight of the creature suddenly thrown upon them.

(3) Mr R. C. BAILEY showed a *band formed by the persistence of an obliterated vitelline artery.* The specimen was taken from the body of an adult male subject in the dissecting-room of the Medical School of St Bartholomew's Hospital. On opening the abdomen a strong band was seen running up to the umbilicus, which on further dissection was found to consist of a fibrous cord, which started from the right side of one of the lower branches of the superior mesenteric artery to the ileum, about a quarter of an inch from the main vessel. It then turned towards the right, crossing in front of the superior mesenteric vein, and lying between the layers of the mesentery. It

Band formed by obliterated remains of the vitelline artery. The anterior abdominal wall is reflected to the right.

crossed the ileo-cæcal junction, being bound down to both these portions of the intestine by the peritoneum, which it raised in a fold.

It then appeared as a free rounded cord, covered by a tube of the serous membrane ; and as it passed up to the navel it pierced the great omentum, just above its free edge, through a rounded ring-like aperture. It was finally lost on the back of the anterior abdominal wall in two peritoneal folds which passed up to the umbilicus.

The cord was undoubtedly the remains of a vitelline artery, and it is interesting to note that there was no trace of a Meckel's diverticulum in connection with it.   Another interesting point about the structure is the way in which it passed through the peritoneum so as to form a free band while still retaining a complete investment from it,—a band so free, in fact, that intestine might easily have been kinked round it, and so strangulated.

(4) Dr DAVID NABARRO showed *two hearts with peculiarities of the great veins*.   In one, the four pulmonary veins entered the right auricle through a large coronary sinus; the other showed a persistent duct of Cuvier (left superior vena cava) which was joined by a left hepatic vein at its entry into the coronary sinus.

A full account of this communication will appear subsequently in the *Journal of Anatomy and Physiology*.

(5) Professor J. SYMINGTON showed a number of beautiful preparations, photographs, and lantern slides to illustrate *the relation of the deeper parts of the brain to the surface*.

(6) Mr KEITH showed a number of lantern slides demonstrating *the extent to which distal segments of the body have been transmuted in the genera of the higher primates during their evolution*.   Mr Keith divided the primates into two groups—the *pronograde* and *orthograde*,—the latter group containing the anthropoids and man.   The pronograde form he assumed to be the primitive type, and accepted extant genera such as Cebus and Semnopithecus as approximate representatives, as far as the number and arrangement of their body segments was concerned, of the Miocene pronograde apes, from which the orthograde was evolved.

In the evolution of the gibbon, the best living representative of the early orthograde form, the caudal vertebræ became amorphous, the depressor muscles of the tail formed a muscular pelvic floor, the 26th segment, instead of being lumbar, became sacral, the origin of the sacral and lumbar nerves was shifted one segment forwards, and the number of sternal ribs reduced.

With the evolution from the early orthograde or gibbon type of the giant orthograde primates—the orang, chimpanzee, gorilla and man—there was a further transmutation forwards, involving a segment or more.   Some of the distal caudal vertebræ and nerves were suppressed; the 25th (lumbar) segment became sacral, the sacral and lumbar nerves were moved forwards in their points of origin.

The statistics and diagrams on which these deductions are based are published in the *Journal of Anatomy and Physiology* for October 1902.

(7) Mr N. BISHOP HARMAN, who had arranged to exhibit a child possessing *the minimal form of fissura facialis*, was obliged to postpone the demonstration of the case on account of the patient's illness.   He showed instead a drawing of the abnormality, which

illustrated the two small recesses in the skin on each side of the face in the vertical lines of the carunculæ, on the right about 3 mm. below, and on the left about 6 mm. below the ·same.   Mr Harman said that the right hole would admit the smallest lachrymal probe (Çouper's No. 1) 3 to 4 mm., the left hole would only admit a bristle for a lesser distance.   The recesses appeared to have no communication with the lachrymal ducts.   It is intended to show the child at a subsequent meeting.

(8) Professor C. J. PATTEN made a preliminary communication on some points on the *topographical anatomy of the thoracic and abdominal viscera of* Hylobates haianus (hainan gibbon).   The animal was first thoroughly hardened by intra-vascular injections of formalin.   The form of the various viscera, which closely resemble those of man, was described.   But the paper dealt chiefly with the position of the viscera relative to the vertebral column.   Besides the actual specimens, two models were exhibited, one of the entire trunk, showing the position of the organs to the vertebral column and ribs; the other, of the duodenum, pancreas, kidneys, adrenals, and spleen, illustrating their form and relations to one another.   This paper will be published *in extenso* at a later date.

(9) Professor A. FRANCIS DIXON exhibited *the skull and some of the long bones* from a case of acromegaly.   In height the individual from whom they were taken was 6 feet $2\frac{1}{4}$ inches   The skull showed in a typical manner great elongation of the face, associated with enormous development of the lower jaw and of the maxilla.   The pituitary fossa was much enlarged, the surrounding bone, owing to absorption, being very thin.   The origins of the temporal muscles were very extensive, the upper limits of the temporal fossæ of opposite sides approaching to within 28 mm. of one another.   The articular surfaces of the long bones were irregular, and exhibited marked arthritic changes.

(10) Professor ARTHUR ROBINSON read a paper on *the preliminary stages of the development of the pericardium.*   The paper, which is published *in extenso* in the October number of the *Journal of Anatomy and Physiology,* may be summarised as follows:—
1. In AMPHIBIANS the pericardium is formed by the fusion of the anterior parts of the lateral halves of the cœlom in the ventral middle line beneath the anterior part of the foregut, and a ventral mesocardium is present for a time.
2. In BIRDS the pericardium is formed after the development of the head fold by the ingrowth of the lateral parts of the cœlom into the ventral wall of the foregut and their fusion in the middle line. The rudiments of the heart lie along the dorsal part of the line of fusion, and for a time a ventral mesocardium is present.
3. In MAMMALS the pericardial mesoderm is present in the pericardial portion of the embryonic area, and it is completely separated into somatic and splanchnic layers before the head fold

appears; there is therefore a single pericardial cavity, which extends from side to side along the anterior boundary of the embryonic area. As the head fold forms, the pericardial region is reversed, and it is carried into the ventral wall of the foregut, where it forms a U-shaped tube, which communicates at each end with the general cœlom.

The rudiments of the heart are formed in the splanchnic layer of the pericardial mesoderm; therefore, after the reversal of the area, they lie in the dorsal wall of the pericardial space, attached by a dorsal mesentery to the ventral wall of the foregut; but they are never at any time connected with the ventral wall of the pericardium by a ventral mesocardium.

(11) *The Sternal Angle in Man.* By WALTER KIDD, M.D.

The adult human sternum presents almost constantly an angle which may be observed through the soft tissues, unless there be an unusual amount of fat or the thorax be an ill-developed one, and it is situated at the junction of the manubrium with the body of the sternum. A projection corresponding to this angle is found along the second costal cartilage and the adjoining portion of the second rib on each side. In a few cases a similar but less pronounced angle is seen at the level of the third costal cartilages. The joint between the manubrium and the body of the sternum constitutes the true sternal angle, and the latter appears[1] to be formed by the deposition of bone on the anterior surface of the joint. The sternal angle corresponds to those transverse lines of junction between the segments of the body of the sternum, the first of which forms the occasional second sternal angle. It is only in advanced age that complete ankylosis takes place in this joint, and therefore much later in life than the other segments become fused.

The sternal angle is sufficiently prominent to have been carefully noted and represented by the sculptors of antiquity, as may be seen in most of the statues in such galleries as those of Rome and Florence, and a very few of these show also the second sternal angle, to which reference has been made. A fairly well defined angle is present in the sterna of the gorilla, chimpanzee, and orang, and of these genera of apes the chimpanzee shows it in the most marked degree.

Such a break as this in the even contour of the sternum must have some mechanical origin, and it seems most probable that it is connected with the difference shown by the first two ribs on the one hand, and the remaining true ribs on the other, as regards their respective directions of movement in respiration. The nearly transverse position of the two first ribs, and consequently smaller degree of rotation, is compensated for by the raising of the sternum in inspiration, which necessarily affects the movement of these ribs more

[1] "The Varieties of Ankylosis by Bone in different parts of the Skeleton," Joseph Griffiths, M.A., M.D., F.R.C.S., *The Journal of Pathology and Bacteriology*, Edinburgh and London, p. 313.

than the others, and greater freedom of movement is afforded to
them by the pre-mesosternal joint.   In this view of the sternal angle
the advantage conferred by the very late ankylosis of this joint is
recognised, and it may be looked upon as a critical level in the thorax,
marking the spot where the expansion of the chest-wall changes
slightly but definitely from one plane to another.   This is recognised
superficially and roughly by placing the chest-piece of a straight
stethoscope on the second costal cartilage while the person examined
is breathing deeply, and then on the third cartilage, when the direc-
tion taken by the ear-piece is clearly seen to bend upwards in the
former case, and either horizontally or downwards in the latter.

The attachments of some of the extrinsic muscles of respiration
round and about this sternal angle bears out the same view of its
production, for, on the one hand, there are the three strong scaleni
muscles elevating and fixing the first two ribs, and on the other, the
triangularis sterni, inserted into the cartilages of the sixth, fifth,
fourth, and third ribs, and slightly and variably into those of the second
and first ribs, depressing the respective costal cartilages.   This is an
arrangement of muscles grouped round the sternal angle, pulling very
much in opposite directions, so that the anatomical conditions calcu-
lated to keep up the movement of the joint under consideration later
than in the rest of the sternum are present.

These simple anatomical statements have been made because they
are necessary to the particular point dealt with here.

In *Nature*, Feb. 13, 1902, I recorded two cases of persons, aged
28 and 33, with especially smooth, hairless skins, who presented
certain isolated hairs standing out from the skin with remarkably
persistent direction.   In one case there were two long hairs, each an
inch and a half in length, just above the sternal angle pointing up-
wards towards the neck ; in the other case there were three hairs,
each an inch long, pointing downwards, and situated just below the
sternal angle.   The only interest in these two cases is the fact that a
few stray hairs, separated from one another in position by less than
the breadth of a costal cartilage, can maintain their original and
divergent directions with such persistence.   These two cases corre-
spond exactly with what is found by a simple study of the hair-
streams on the pectoral region (see figure).   The arrangement is re-
markable, and confined, as I believe, to man alone.   At the level of
the sternal angle there occurs a division of the hair-streams, by which
one pursues its normal and ancestral course down the sternal groove
and over the pectoral muscles, and the other stream divides from it
at the level of the sternal angle, and passes vertically upwards to the
neck in the middle line, and over the clavicles it slopes towards the
middle line till it reaches the level of the upper border of the larynx,
where its course need not be pursued.

An arrangement of hair so peculiar as this at the level of the
sternal angle (which I may repeat is not shared by any other animal
possessing a sternal angle) is almost certainly connected with the
function of respiration in some way or other.   But inasmuch as this
hair arrangement is not found in man's nearest existing congeners,

although they too possess a sternal angle, some other ætiological factor must be sought for it. I would suggest that the effect of the pressure of clothing on the underlying skin is competent to produce this change in the direction of the hair, and that probably it is the efficient cause. During inspiration in the sitting and standing postures, or in locomotion, the weight and friction of clothing on the upper portion of the chest-wall clearly tends to pull on the ever-growing stream of hair, drawing it over the sternum upwards, and in the subclavicular region upwards and towards the middle line. In expiration the chest-wall is almost entirely removed from any
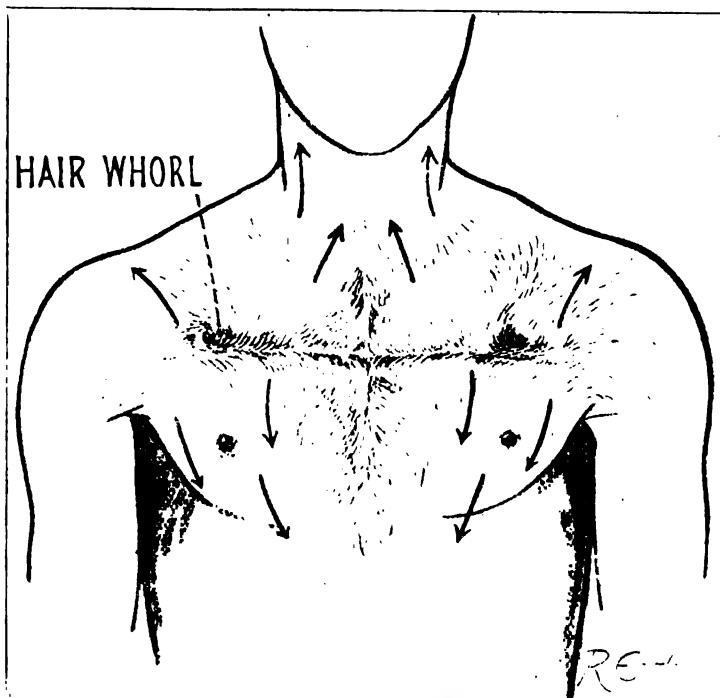
pressure or friction of clothing, so that any reverse action on the hair-stream, which might be supposed to be exercised by expiration, does not take place. Below the joint which forms the sternal angle the changing direction of the ribs during respiration is not calculated in the same degree to draw the stream of hair upwards and contrary to its ancestral trend.

[Wiedersheim touches on this subject in his *Structure of Man*, translated by H. and M. Bernard, 1895, pp. 22, 23, 24, 25, which I had not seen at the time of writing this paper. He there refers the whorls found on the pectoral region of man to the supernumerary

teats occasionally found above the normal mamma, and quotes two
cases from Herr Otto Ammon, one with a single pair and the other
with three pairs of supernumerary teats. The former showed these
whorls in the region of the teats above the normal mamma, but
Wiedersheim makes the significant admission that those *below* that
situation do not form vortices. This is exactly what would be ex-
pected, for the arrangement which I have indicated is simply the
normal one found in all persons who are sufficiently hairy. It has
nothing to do with supernumerary teats.]

(12) Professor A. MACPHAIL demonstrated a case of *rudimentary first
dorsal ribs* which had been brought under his notice in the dissecting-
room of the University of Glasgow. The macerated vertebral
column with the abnormal ribs articulated, the second pair of ribs,
the sternum, and two drawings (figs. 3 and 4) illustrating the condition
of the soft parts, were exhibited.

The subject was an adult male Kaffir, in all other respects of a very
well developed type. The clavicles had been disarticulated and the
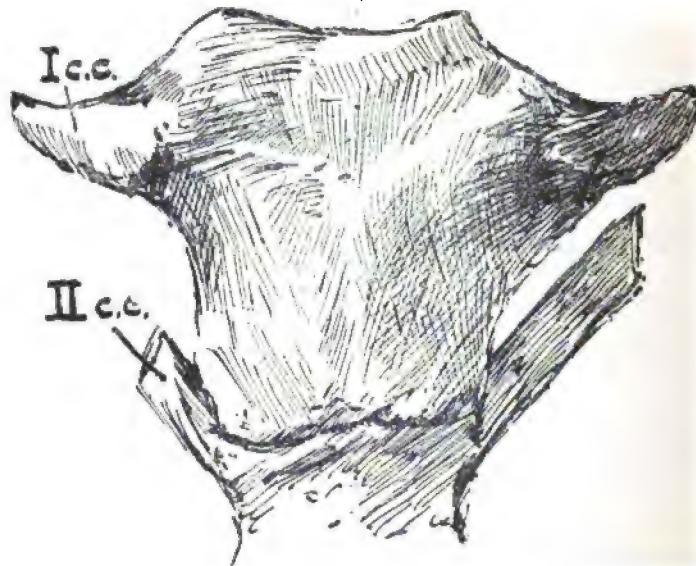
FIG. 1.—Sternum with second and vestigial first costal cartilages attached.

costal cartilages cut through for the removal of the sternum before
the abnormal condition of the first arch had been observed, so that it
was impossible to determine accurately the relations of a vestige of
that arch in connection with the manubrium sterni on each side.
This seemed to take the form of an irregular block of partly ossified
cartilage, to which the subclavius muscle was partly attached, and

which deepened the clavicular surface of the sternum on its external and inferior aspect. The maceration of the specimen in sand destroyed the cartilaginous part of these blocks, leaving, however, a small ossified mass on each side, which, on being connected to the sternum beneath the clavicular surfaces, gave a complete transverse measurement of 10·5 cm. to the bone at that part. The inner end of each clavicle, corresponding to this increased surface, is likewise enlarged, measuring 3·5 cm. in an oblique antero-posterior direction; this abnormal extent of the sternal end of the clavicle is gained principally by a somewhat hook-shaped projection of the articular surface downwards and backwards, and this part was found, in the recent condition, to rest against the vestige of the first costal arch described above, which, thus modified, has increased the strength of the sterno-clavicular articulation.

The following points were noted in the relations of the soft parts before maceration :—

The tendon of the subclavius muscle on each side was principally
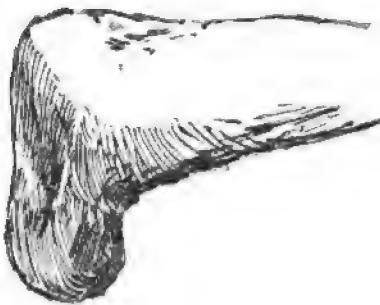
Fig. 2.—Sternal end of left clavicle.

attached to the tip of the second rib and its cartilage, but was also connected by means of strong fibrous tissue to the 'vestigial' cartilage of the sterno-clavicular articulation.

The anterior extremity of the 1st rib presented as a pointed process among the fibres of the scalene muscles, and there was no trace of any fibrous band continuing its direction forwards, such as has been described in other records of similar abnormalities. The right rib being considerably larger than the left, it reached a lower level in the neck, and was placed beneath the arch of the subclavian artery, while the extremity of the left rib was situated immediately above the level of the highest point of the arch.

On the right side only some fibres of the scalene group lay in front of the artery in the position of the scalenus anticus; these arose from the anterior tubercle of the 6th cervical vertebra, and passed down as a thin slip in front of the artery, to be inserted into the outer (upper) surface of the second rib : a slight pointed tubercle marks this attachment in the macerated specimen. A slip similar in

origin was present on the left side, and was traced downwards behind
the artery to the second rib.

A few tendinous slips arising from the anterior tubercles of the 3rd,
4th and 5th c.v. formed a thin sheet passing to be inserted into the tip
of the 1st rib on each side, while the rest of the scalene mass arising
from the posterior tubercles of the lower cervical vertebræ formed a
muscular sheet, partly inserted into the rudimentary first rib, but
mostly into the upper surface of the second.

A fan-like sheet of muscle radiating from the tip of the 1st rib and
inserted into the upper surface of the 2nd rib represented the external
intercostal muscle of the first space. There was no trace of an in-

ANTERIOR
EXTREMITY
OF
FIRST RIB
(RIGHT)

ANTERIOR
EXTREMITY
OF FIRST
RIB
(LEFT)

FIG. 3.

ternal intercostal muscle ; in its place on the right side there was a
well marked membranous sheet, with some aponeurotic fibres joining
the first to the second rib.

The anterior extremity of the first rib on each side was bound to
the second by a cone-shaped ligament, extending almost transversely
outwards, and overlapping the external intercostal sheet.

The cords of the brachial plexus were normal on both sides as
regards contributing nerves ; the lower cord lay immediately behind
the subclavian artery on the right side, while the corresponding cord
on the left was displaced upwards by the projecting extremity of the
first rib, and was separated by it to some extent from the artery. In

addition to the vestigial cartilage at the sterno-clavicular articulation, seven costal cartilages articulated with the sternum : the cartilages of the second arch were more obliquely placed than normal, particularly that of the right side ; the cartilages of the eighth arch thin at their extremities, and to a large extent united to those of the seventh, were traced to the margin of the sternum.
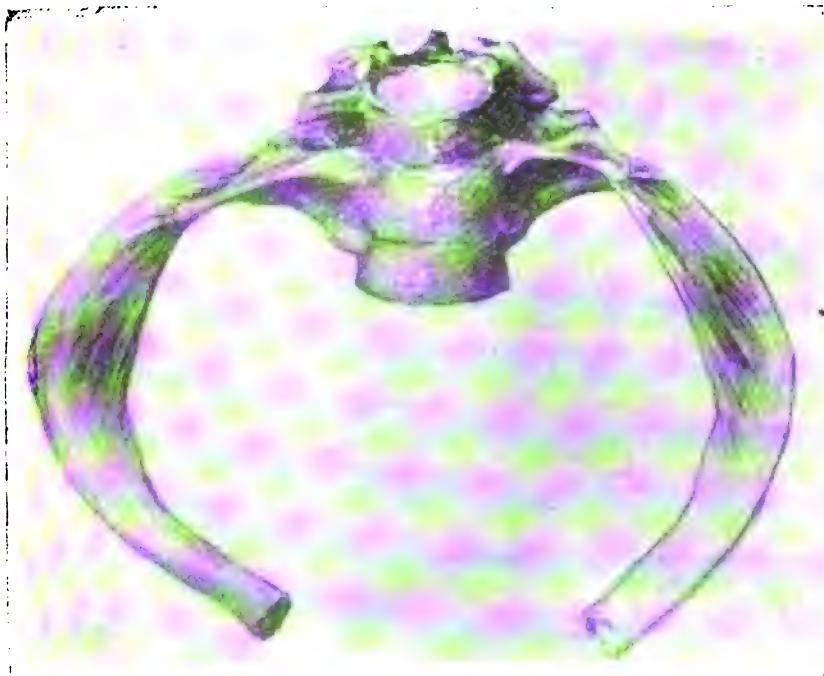
FIG. 4.

After maceration the following measurements were made :—

First Rib : *Right*—Entire length 5 cm. ; length from inner edge of head to outer edge of tubercle 3·5 cm.; breadth at tubercle 2 cm.

Left—Entire length 3·5 cm. ; length from head to tubercle 3 cm. ; breadth at tubercle 2 cm.

(The transverse processes of the first dorsal vertebra showed a corresponding difference in length.)

Second Rib : *Right*—Length from head to tubercle 3 cm. ; length from tubercle to anterior extremity 15·2 cm. ; greatest transverse breadth 2·5 cm.

Left—Length from head to tubercle 2·6 cm. ; length from tubercle to anterior extremity 4 cm. ; greatest transverse breadth 2·3 cm.

Both these ribs lie more horizontally than a normal second pair and their shafts are distinctly flattened, resembling, both in position and shape, an enlarged first pair. The transverse diameter of the upper opening of the thorax measured (approximately) 18 cm.

A full account of the bibliography connected with this condition was published in the *Proceedings* of the Society, May 1900, by Phillips; this appears to be the sixth case of the kind recorded in Britain.

(13) Mr R. K. SHEPHERD, B.Sc., read a communication on " The Form of the Human Spleen." The paper is published *in extenso* in the October number of the *Journal of Anatomy and Physiology.*

(14) At the meeting of the Society held at Charing Cross Hospital Medical School on Friday May 9th, Dr C. ADDISON showed *three museum preparations* to illustrate the method of preparing specimens by immersing them for various periods in a solution of bleaching powder, to bring out with more distinctness ligamentous and fibrous structures.

Dr Addison also showed a specimen taken from a dissecting-room subject which presented a *cervical rib on each side*. The subject was a female æt. 56.

There were twelve thoracic ribs, the 12th rib on each side being much reduced in size. The cervical ribs articulated with the body of the 7th cervical vertebra, and with the posterior segment of the transverse processes in the manner usually described.

From the head of the tubercle the cervical ribs measured 2·5 cm. and 2·7 cm. on the right and left sides respectively. From the tubercle each rib arched forward parallel with the first thoracic rib, and gradually narrowed to a blunt point, measuring from the tubercle to the extremity along the outer border 3·5 cm. and 7·5 cm. on the right and left sides respectively.

From the extremity of each cervical rib a fibrous cord (measuring 5·5 cm. and 4 cm. on the right and left sides respectively) was prolonged forwards to a bony projection which extended outwards from the first piece of the sternum below the clavicular articulation, and which, in a large measure, as shown in the diagram, occupied the usual position of the sternal end of the first thoracic arch. This projecting piece of the sternum measured 3 cm. on the right side and 1 cm. on the left from the outer margin of the clavicular articulation. It presented the most unusual feature of the case, and is especially interesting in regard to the possible development of the sternum in conjunction with the costal arches.

The sterno-clavicular articulation was normal on both sides, with well developed inter-articular fibro-cartilages. The first thoracic rib had a costal cartilage commencing about the usual place, which at its sternal extremity was not embedded into the manubrium sterni as usual, but articulated, with a synovial joint, with the lower surface of

the bony process projecting from the sternum, and the costal cartilage gradually tapered to a blunt point at its sternal end.

The musculature of the specimen did not differ materially from other recorded cases. Between the cervical costal arch, made up of the rib and fibrous cord on each side, and the first thoracic rib there were well marked external and internal intercostal muscles and a small sub-costal muscle on each side in series with the rest.

The scalenus anticus on the left side was inserted into the upper border of the cervical rib near its tip, and on the right side for 1·5 cm. into the fibrous cord springing from the cervical rib, and for ·5 cm. into the tip of the rib itself, which, it will be remembered, was smaller than on the left side. Behind the scalenus anticus on each side the subclavian artery and the lowest cord of the brachial
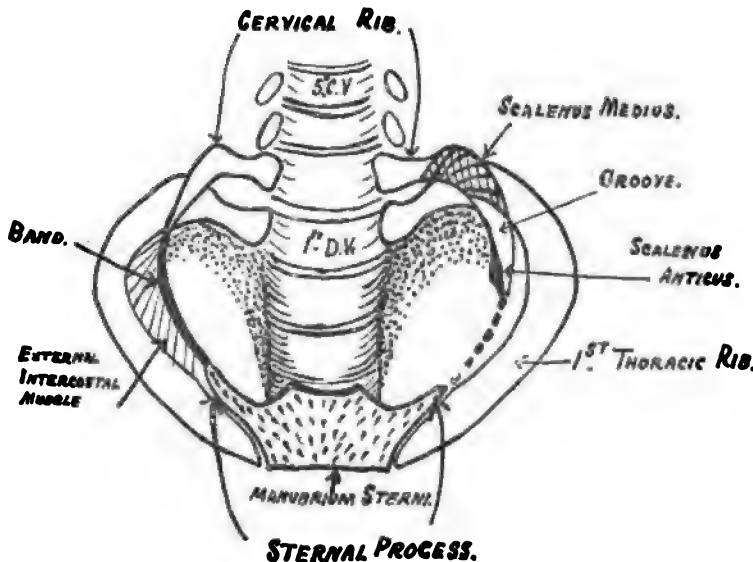
plexus grooved the upper surface of the additional rib. The front part of the scalenus medius on each side was inserted into the upper surface of the cervical rib from the groove in front to the tubercle behind, whilst the back part of the muscle terminated in the intercostal tissues between the cervical and first thoracic ribs, with a fibrous extension downwards to the upper border of the first thoracic rib. The scalenus posticus was wholly inserted into the outer surface of the first thoracic rib on the left side. On the right side it was partly attached to the first thoracic rib and partly prolonged across the first thoracic intercostal space to the upper border of the second thoracic rib.

There was no abnormality in the arrangement of the subclavian

arteries or their branches, or of the cervical nerves, or in their relations to the scalene muscles.

Unfortunately, at a late stage of the dissection, the fibrous cord prolonged from the left cervical rib was cut away, and the innervation of the additional muscles and costo-vertebral articulations could not be worked out.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN

AND IRELAND.

NOVEMBER 1902.

THE Annual General Meeting of the Society was held at King's College, Strand, W.C., on Friday, November 14th, at 4 p.m. The President, Mr C. B. LOCKWOOD, was in the chair, and nineteen members and one visitor were present.

The minutes of the last meeting were read and confirmed.

The following officers were then elected for the ensuing year :— ·*President*—C. B. Lockwood. *Vice-Presidents*—Arthur Thomson, M.B.; A. M. Paterson, M.D.; J. Yule Mackay, M.D. *Treasurer*— G. B. Howes, LL.D., F.R.S. *Secretaries*—Peter Thompson, M.D. (England); R. J. A. Berry, M.D., F.R.S.E. (Scotland); N. H. Alcock, B.A., M.D. (Ireland). *Council*—C. Addison, M.D.; A. Birmingham, M.D.; J. Black, M.B.; T. H. Bryce, M.D., F.R.S.E; D. J. Cunningham, M.D., F.R.S.; A. F. Dixon, M.B.; E. Fawcett, M.B.; R. J. Gladstone, M.D.; T. Wardrop Griffith, M.D.; A. Keith, M.D.; R. C. Lucas, M.S.; J. Musgrove, M.D.; F. G. Parsons; C. J. Patten, M.D.; W. G. Ridewood, D.Sc.; Arthur Robinson, M.D.; Barclay Smith, M.D.; J. Symington, M.D.; G. D. Thane; B. C. A. Windle, M.D., F.R.S.

The Treasurer's Report, showing a balance in hand of £85, 13s. 6d., was received and adopted. In presenting the report, the Hon. Treasurer remarked that one satisfactory feature of the balance-sheet was the fact that the income for the year had slightly exceeded the expenditure, which had not always been the case in the past. Referring to the recovery of arrears, he pointed out that the amount thus received had brought the balance in hand up to a sum which throughout his twelve years of service had been but once before approached. He was proud of it, as it marked the recovery of arrears of six to eight years' standing, almost despaired of. It was the more welcome, now

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that the Society would probably embark on a new bibliographic venture, and would during the year have to meet the major part of the cost of production of the MS. index to vols. 31–40 of the *Journal of Anatomy and Physiology*, now well advanced.

The following candidates were elected members of the Society :— S. C. PAUL, F.R.C.S., Lecturer on Anatomy, Ceylon Medical College, Colombo, proposed by Arthur Robinson, Peter Thompson, E. J. Jenkins. JOHN CAMERON, M.B., Ch.B., M.R.C.S., Bute Anatomy Department, University of St Andrews, Fife, N.B., proposed by James Musgrove, G. D. Thane, Peter Thompson.

A Report was next read by the Honorary Secretary for England which had been received from Prof. G. D. THANE, the Chairman of the Committee appointed to deal with the supply of slips of items relating to anatomy, to the International Catalogue of Scientific Literature. The slips for 1901 are now completed, and to enable the work to be carried on it was decided that the sum of £10 be placed at the disposal of the Committee.

Specimens and Papers :—

(1) Dr R. N. SALAMAN showed a specimen of *Volvulus affecting that tract of the small bowel developed from the anterior segment of the primitive intestinal loop.* The specimen was from a child which died three days after birth. The mesentery of the small bowel was only attached round the superior mesenteric artery. The coils of the intestine had become twisted round a pedicle represented by the vasa intestini tenuis. This had led to occlusion of the vessels and gangrene of the bowel. The part of the bowel developed from the posterior segment of the loop—that part distal to Meckel's diverticulum —was normal in form and unaffected.

(2) Mr KEITH showed a specimen of *Volvulus formed by the cæcum, ascending colon, and terminal part of the ileum.* The bowel had become twisted round a pedicle represented by the ileo-colic artery. The condition was due to the absence of a meso-cæcum and meso-ascending colon.

(3) *The Anatomy of the Valvular Mechanism round the Venous Orifices of the Right and Left Auricles, with some Observations on the Morphology of the Heart.* By ARTHUR KEITH, M.D.

Introductory.—It is evident that the orifices of the great systemic veins which terminate in the right auricle, as well as those of the pulmonary veins in the left auricle, must be closed at the commencement of each auricular contraction, otherwise the force of the

contracting auricles would be spent as much in returning the blood to the veins as in passing it on to the ventricles.

Some years ago my colleague Dr Leonard Hill, F.R.S., told me that he was convinced, from observations he made while carrying out experiments on the circulation, of the presence of a valvular mechanism at the terminations of the venæ cavæ in the right auricle. At the time I could not suggest the anatomical basis of such a mechanism.

Recently, while investigating the anatomy of the diaphragm and verifying the action of its several parts in the living by the aid of Röntgen rays, I was struck by the mass of the right crus and its insertion—indirectly, it is true—to the termination of the inferior vena cava and pericardium (see fig. 6). It was evident that the contraction of the right crus of the diaphragm—constituting one fifth of the total weight of its muscle—was expended on the heart. It was easy to see that it could exert, to a certain extent at least, a constricting influence on the venous orifices of the right auricle; but further investigation showed that while the presence of the right crus of the diaphragm was necessary for the closure of the venous orifices of both right and left auricles, yet the mechanism whereby these orifices were closed lay in the walls of the auricular chambers.

Statement of Results.—

1. That at the commencement of each auricular systole the systemic and pulmonary venous orifices are closed, and the parts of the auricles derived from sinus venosus in the right and left auricles are shut securely off from the true auricles by certain bands of muscle.

2. That in valvular diseases of the heart, which lead to back pressure of the blood in the auricular chambers, the muscular valvular mechanism which closes the venous orifices at first hypertrophies and remains competent; as long as this is the case no serious symptoms are manifested. When the disease has proceeded to an extent which leads to a destruction and atrophy of the valvular mechanism, then all the worst symptoms of heart disease appear. Further, as that part of the mechanism which surrounds the termination of the inferior vena cava is the most delicate, it is the first to break down. That round the superior vena cava is so strong that I doubt if it ever becomes incompetent. The mechanism of the superior pulmonary veins of the right and left lungs is stronger than that of the two inferior veins.

3. The arrangement of the musculature of each auricular chamber is such, that when the vestibular part—that part of the auricle derived from the sinus venosus—is shut off from auricle proper, the auricular appendix is pulled until it lies over the base of its corresponding ventricle, with its mouth directed against the corresponding auriculo-ventricular orifice. The structure of the appendix gives the contraction of its muscle a hydraulic effect; by its contraction the ventricle receives the final complement of its load.

4. All the elements of the reptilian heart can be identified in the avian and mammalian heart; and although the manner in which these

elements are combined differs somewhat in the reptilian and
mammalian heart, yet the function of each element remains constant.
The heart may be defined as the most conservative organ of the
body; it has always served the purpose of a pump; the only
alteration it undergoes from one end of the vertebrate kingdom to
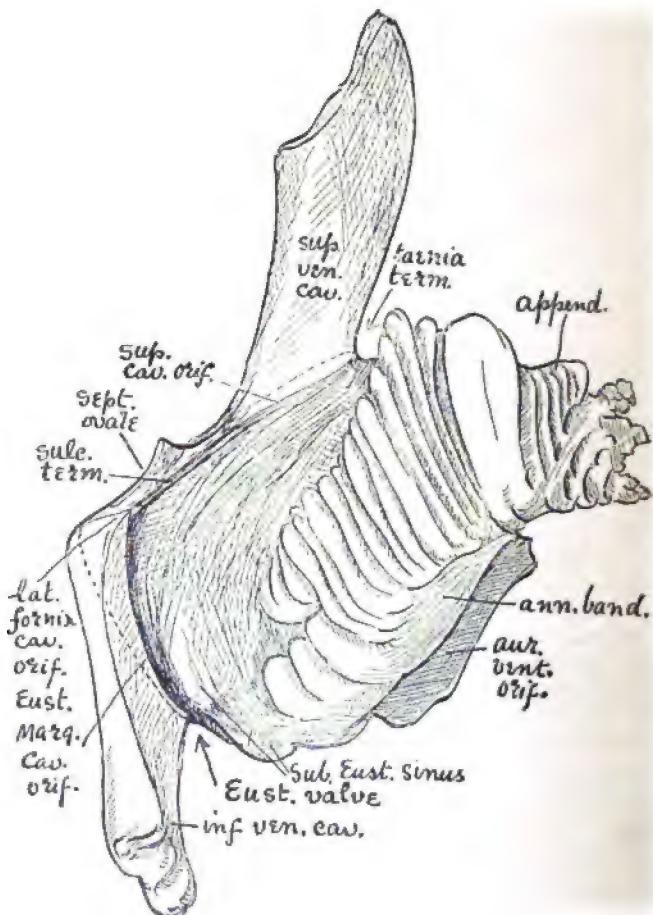
FIG. 1.—Wax cast of the right auricle of a child's heart (1 year old) viewed from
    the right lateral aspect. The cast represents the shape of the right auricle
    when contraction has just commenced.

the other is due to an alteration in the manner by which the blood
is arterialised.

5. The functional value of the various elements described by His
and Born as taking part in the separation of the right and left

chambers of the heart can be recognised by a study of the evolution of the vertebrate heart, and the observation of both men, apparently discrepant, reconciled.   That while His and Born are undoubtedly correct in their observation of fact, they probably err in the interpretations of these facts.   Both men regard the various septa of the heart as ingrowths from the wall of the primitive cardiac tube.   While to a certain extent this may be true, yet it is impossible to account for the form and structure of the vertebrate heart, and the many malformations to which it is subject in man, except on the supposition that the auricles proper and the ventricles are outgrowths from the primary cardiac tube—in fact, these chambers appear on the cardiac tubes as soap-bubbles are blown from the bowl of a pipe.

Methods employed.—

1. Of the various methods which have proved advantageous in this investigation, the most profitable has been the study of the *heart in situ*, and especially by exposing it from behind by removing the lower dorsal and upper lumbar regions of the spinal column.

2. By the use of "heat-contraction"—by availing myself of the well known fact that the application of a substance at the boiling-point of water to a dead muscle causes it to undergo a contraction which is physically similar to a normal contraction in life.   By applying a steam-jet to a muscular fasciculus, an approximation to its normal contraction is obtained.   By pumping water near its boiling point into a *heart in situ* the various chambers, but especially the thin-walled auricles, are thrown into a state of contraction.   By injecting molten paraffin wax at a temperature of boiling water, casts of the auricular chambers in various degrees of contraction may be obtained—a method which I find has been already employed by Hasse.

3. By studying the action of the various muscular fasciculi of the auricles when these fasciculi are traced on casts of the auricular chambers.   This is a method of investigation of the greatest advantage in the study of all hollow muscular viscera.   The cast represents the load of the viscus; when the various muscular fasciculi are traced on the cast, then one can see the part played by each fasciculus in discharging the load of its viscus.

4. By verifying all the conclusions arrived at from a study of the normal human heart, (*a*) on the human heart in pathological conditions, (*b*) on the malformed human heart, of which there is a rich collection in the London Hospital Museum, (*c*) on the splendid "comparative series" of hearts in the Museum of the Royal College of Surgeons of England, (*d*) on to the models of the development of the human heart by His and Born.

The venous orifices of the right auricle.—It is necessary to give a short description of the three venous orifices of the right auricle— superior caval, inferior caval, and coronary, for the accounts given in text-books are not accurate enough to serve my present purpose. References to figures 1, 2 and 3 will make my description easier to understand.

(a) *Superior caval orifice.*—The superior caval orifice is elliptical in
shape, with an anterior, right or *Eustachian*, and a posterior, left or
septal margin.   The margins meet at a left or *mesial* and at a right
or *lateral* fornix, the latter being situated at a much lower level—as
regards man in the upright position—than the mesial fornix (see fig 3).
The position and relationship of the mesial fornix, which is rounded in
shape, requires careful definition.   It will be observed (see fig. 2)
to be situated at the angle where the anterior or *aortic* wall of the
left auricle, and the mesial or *aortic* wall of the right auricle, join
with the interauricular septum.   To this junctional angle, which is
a constant feature of mammalian and avian hearts, it is necessary to
refer again and again.   It is always situated over the posterior or
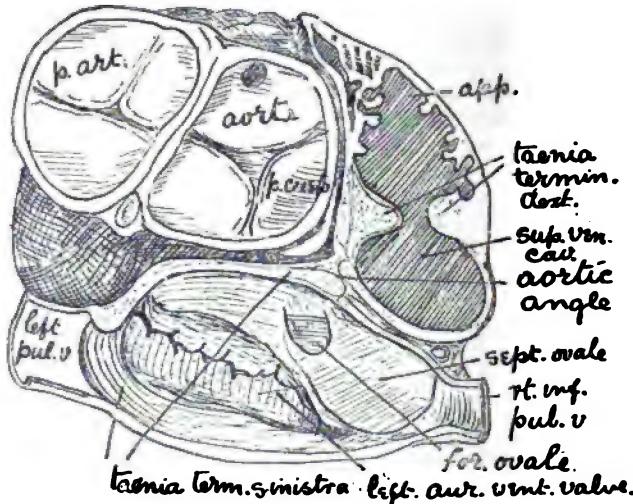
Fig. 2.—Horizontal section of the heart to show the aortic angle of the auricles
and the relationship of the superior vena cava to the two auricles.

dorsal cusp of the aortic semilunar valve.   The angle in which the
aortic walls of the two auricles fuse with the interauricular septum
may be named the *aortic angle* of the auricles (fig. 2).
    The superior caval orifice is closed by the anterior or Eustachian
margin being brought firmly against the septal margin.
    (b) *The inferior caval orifice.*—The inferior caval orifice is also
elliptical in shape, with an anterior, right or Eustachian, and a posterior,
left or septal margin.   The two margins terminate at a left or mesial
fornix, and a right or lateral fornix, which is situated at a much higher
level—in the upright posture—than the mesial fornix (fig. 1).   The
mesial fornix is situated at the inner or mesial angle of the base of
the septum ovale, the outer fornix at the lateral angle of the base of
the septum (fig. 4).

The inferior caval orifice is closed by the anterior or Eustachian margin being brought in contact with the septal margin.

The sulcus terminalis.—It will be seen (see fig. 3) that the lateral fornices of the superior and inferior caval orifices approach each other on the lateral wall of the auricle, being a little less than one inch apart in the normal human adult heart. The lateral fornices are connected by the sulcus terminalis (His), an indifferently marked fibrous septum which marks the line at which that part of the sinus
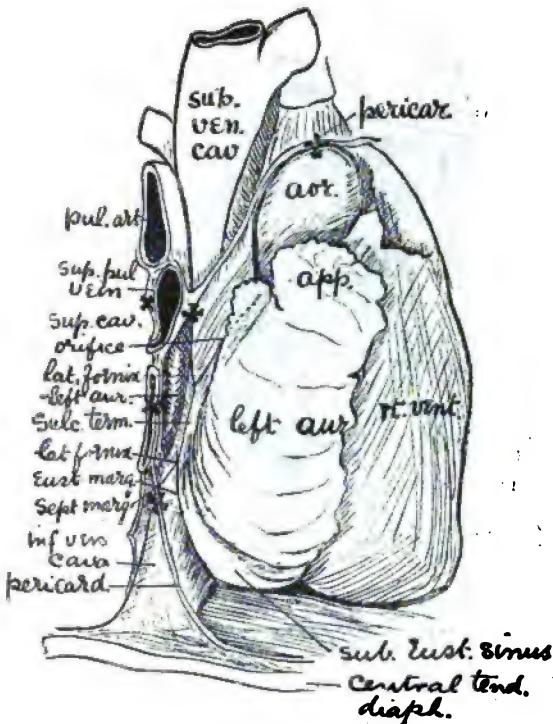
FIG. 3.—Heart of an adult viewed from the right lateral aspect, to show the manner in which the venæ cavæ terminate in the right auricle. The crosses mark the points which are fixed during the contraction of the heart.

venosus which connected the superior and inferior venæ cavæ in the fœtus, sunk within and was overgrown by the proper auricular musculature. The distance between the lateral fornices of the caval orifices is scarcely altered in contraction of the auricle.

The relationship of the septum ovale and annulus ovalis to the inferior caval orifice.—The base of the septum ovale is continuous with the septal margin of the inferior caval orifice, and hangs over that opening like a partially opened lid (see figs. 8 and 11). The lower or right surface looks into the lumen of the inferior vena cava,

and towards the crest of the right ilium. While the base of the septum ovale is fixed or hinged to the septal margin of the inferior caval orifice, its convex margin is overlaid by the annulus ovalis. The annulus is made up of two distinct parts, differing in origin and in function. The inferior limb of the annulus, referred to afterwards as the *inferior limbic band*, starts from the mesial fornix of the inferior caval orifice, and ends in the aortic auricular angle and in the central fibro-cartilage (see figs. 4, 7, 9, 10, 11). The superior limb of the annulus, the *superior limbic band*, begins at the lateral fornix of
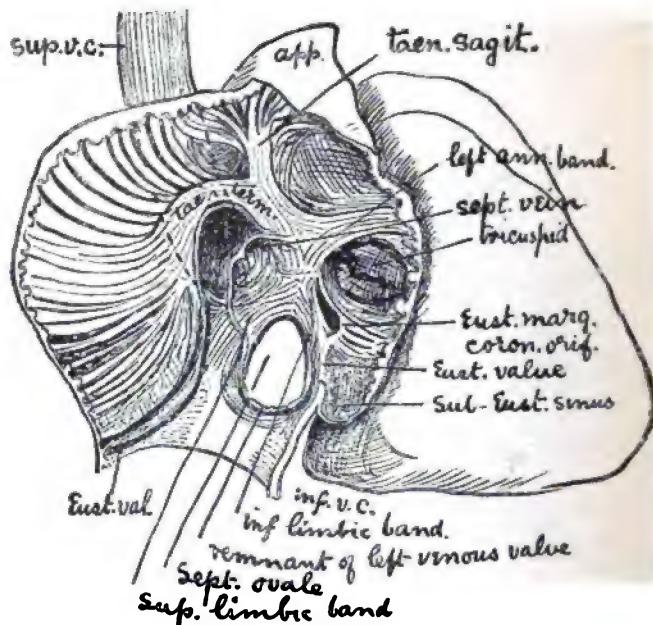
Fig. 4.—The right auricle of the heart of a child 4 years old is thrown open. The Eustachian margin of the inferior vena cava is thrown outwards, and the musculi pectinati divided just above their union with the left annular band.

the caval orifice and terminates in the aortic auricular angle (see figs. 2, 4, 11). The part played by these two bands in closing the inferior caval orifice will be explained presently; it is necessary to describe their situation to make the description intelligible. Further, the septum ovale enters into the formation of the anterior or ventral wall of the left auricle.

(c) *Coronary orifice in the right auricle.*—This orifice, situated at the base of the interauricular septum, is also elliptical in shape, with an anterior, right or *Eustachian* margin, a posterior, left or *septal* margin, these margins terminating at a mesial and a lateral fornix

(fig. 4). It also is closed by the approximation of the Eustachian to the septal margin.

These three venous orifices open in the *vestibule* of the right auricle—that part of the auricle derived from the right sinus venosus. It will be more strictly defined at a later stage of this paper.

duct art.

sup. ven. cav
azy. v.
rt pul. art
rt sup. pul. v.
fibres of sept.
expan.
sph. fibres
ven. cav.
sulc. term.
inf. left. pul
vein
inf. ven. cav.
fibres of sup. limb
fibres of inf limb
pericard.
diaph.

fold of
Marshall

app.

vestibule

atrium

lft. vent

hep. veins

Sub. Eust. sinus

left taenia termin

cor. sinus
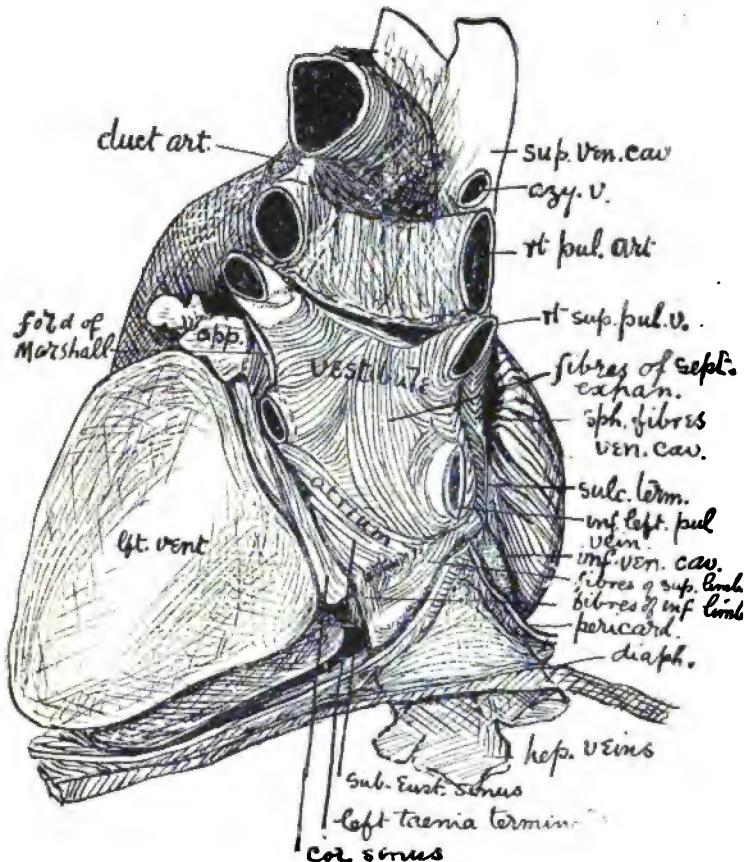
Fig. 5.—A dissection of the heart from behind to show the arrangement of the muscular fibres of the left auricle and the relationship of the auricle to the inferior vena cava. To be compared with fig. 6.

The position and shape of the venous orifices of the left auricle.— A reference to fig. 5 will make the brief description given here intelligible. The left auricle, like the right auricle, is made up of three parts, each of which serves a separate purpose in the auricular systole. The first of these parts is the *vestibule*, the part derived

from the left sinus venosus, and into which the pulmonary veins pour
their blood.   It is completely separated from the rest of the auricular
chamber in systole.   The second part is the auricular appendix.
The third part is the atrium into which the appendix and vestibule
open (figs. 5, 11).   The atrium descends into an *angular recess*
situated between the septum ovale, the posterior or left margin of
the left auricular ventricular orifice, and the vestibule (see fig. 11).

   The *vestibular* part, into which the pulmonary veins open, is nearly
square in outline, as seen on the dorsal aspect of the heart (fig. 5).
Its posterior or *dorsal* wall is nearly stationary during the contraction
of the auricle ; the interauricular septum and aortic wall of the left
auricle become then applied to it (fig. 11).   In the systolic phase,
the posterior wall presents a sharp upper margin, passing from the
right superior pulmonary vein to the left superior vein (fig. 5).

   In each of the four angles of the vestibule of the left auricle is
the opening of a pulmonary vein (figs. 5, 6).   The superior angles
are more elongated than the inferior.   Until the pulmonary veins
perforate the pericardium, they are destitute of striated muscle fibres.
The pulmonary venous orifices are elliptical in shape, with posterior
or dorsal and anterior or ventral margins.   The musculature round
their terminations does not possess a sphincter-like action, but closes
the pulmonary orifice by the approximation of their two margins.

   The fixed points at auricular base of the heart.- Before proceeding
to describe the manner in which the venous orifices of the auricles are
shut, it is necessary to direct attention to the manner in which
certain parts of the auricular chambers are fixed in position.   These
fixed points are the bases from which the muscle bands act in closing
the venous orifices.   If the muscular bands are detached from their
points of fixation, then they can no longer exert such an action.
Hence the necessity for studying the heart *in situ*.

   (a) *Fixed points of the venous orifices of the right auricle.*—There
are two such points for the right auricle (see figs. 3, 6).   The lateral
fornix of the inferior caval orifice is fixed firmly to the central tendon
of the diaphragm and indirectly to the right crus.   The lateral fornix
and the right or lateral margin of the terminal part of the superior
vena cava are fixed to all those structures of the middle mediastinum
which form the root of the lung (fig. 3).   By the fascial tissue round
the superior vena cava, the lateral fornix of the superior caval orifice
is fixed indirectly to the upper aperture of the thorax.   The dorsal
part of the pericardial sac passes from the lower to the upper of
those fixed points, and maintains them in relatively the same
relationships in all stages of a respiratory cycle (see figs. 5, 6, 7 and
16).   It should be noted that the mesial fornices of the caval
orifices, unlike the lateral, are free, and it is these mesial parts of the
caval orifices that undergo the greatest amount of movement and
contraction during the systole of the auricle.   The points of fixation
are confined to the vestibule of the right auricle.

   The fixed points of the left auricle.—The sinus obliquus of the peri-
cardium passes up behind and covers the whole of the posterior wall

of the vestibule of the left auricle (figs. 5 and 6).   Its upper
boundary corresponds to the superior margin of the vestibule, which
lies between the right to the left superior pulmonary vein (fig. 6).   Its
left boundary is formed at the left margin of the vestibule of the
auricle, and passes from the superior to the inferior left pulmonary
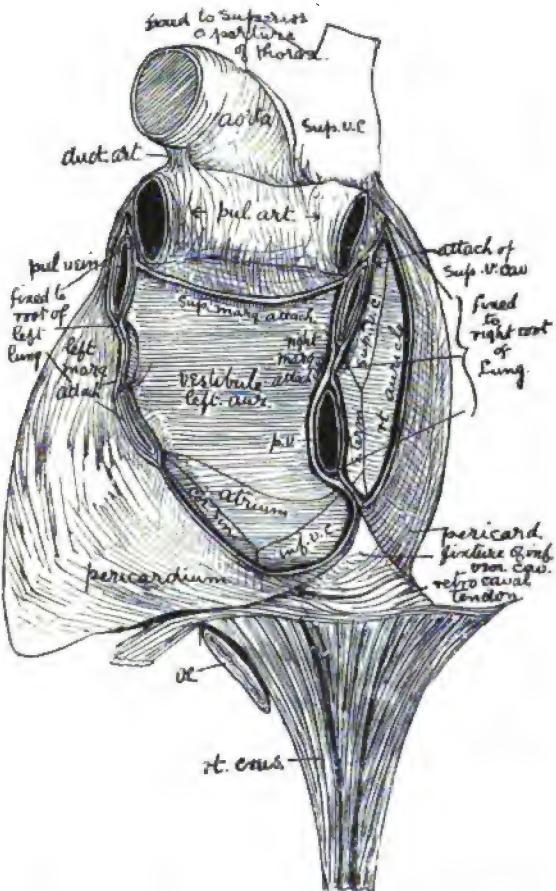
FIG. 6.—A dissection of the heart from behind to show its points of attachment.
Two windows have been made in the pericardium to show the right and left
auricles.   The diagram shows how the right crus of the diaphragm acts on
the base of the heart and roots of the lungs.

vein.   Its right boundary corresponds to the right margin of the
vestibule, which passes from the superior to the inferior right pul-
monary vein.   These three margins of the *vestibule* of the left aruricle
are fixed.   The three lines of attachment may be described as *left
marginal*, *superior marginal*, and *right marginal*.   By the right

marginal attachment the vestibule is fixed to the root of the right lung, and through the lung to the whole right parietal wall of the chest. By the left marginal attachment, to the root of the left lung and left wall of the thorax. By the superior marginal attachment it is fixed to the pulmonary arteries and the bronchi. If these three attachments are destroyed, then the musculature which closes the vestibule of the left auricle can no longer act.

Further, it is to be noted that the right marginal attachment is continuous above with that of the right margin of the superior vena cava, below with that of the inferior vena cava (fig. 6).

The action of the right crus of the diaphragm on the pericardium and heart.—The fixed points I have described belong to two quite distinct classes. They may be distinguished as inferior or *diaphragmatic* and superior or *pulmonary*. All three attachments of the left auricle belong to the latter set, and so does that of the superior caval orifice. The inferior caval orifice is the only one fixed to the diaphragm, and this attachment is found in all mammals. The more extensive attachment of the pericardium to the diaphragm found in animals adapted to an upright method of progression, such as man and the anthropoids, is a result of their adaptation to that posture. The primitive and essential attachment to the diaphragm is that at the lateral fornix and lateral margin of the inferior vena cava. At the diaphragmatic attachment of the heart terminates the massive fibres of the right crus (fig. 6). The superior attachments are bound to the inferior by the posterior or dorsal wall of the strong fibrous pericardium and by the right marginal attachment of the left vestibule (fig. 6).

A reference to figs. 7 and 16 will show that the posterior wall of the fibrous pericardium is essentially a tendon by which the right crus of the diaphragm acts on, not only the inferior caval orifice, but also on the upper auricular attachments and roots of the lungs.

This conclusion was arrived at from a consideration of the anatomical arrangements of the parts. A prolonged examination of the action of the diaphragm in life, by the aid of Röntgen rays, showed that the conclusion was right. In each inspiration the base of the heart, the roots of the lungs and their constituent parts are moved downwards and forwards, so that the base of the heart is separated by a greater space from the spinal column. When one thinks of it, the matter becomes really one of common-sense, for it is quite evident that, to allow expansion of the lungs to take place on inspiration, their roots must move downwards and forwards to allow such an expansion to take place. The lungs can expand only to a slight degree in an upward or backward direction, owing to the immobility of these parts of the chest wall.

The 'respiratory pump' action of the right crus.—The right crus not only maintains the fixed points of the auricles in their proper relative positions during the various respiratory movements of the heart, but it is the most essential part of that mechanism which has been described by Dr Leonard Hill as the 'respiratory pump.'

A reference to fig. 7 will assist me in making clear one of the most

ingenious adaptations in the organisation of the body, and which, as far as I know, has not attracted much attention.   The inferior cava (fig. 7) lies between the liver in front and the right crus behind.   At the commencement of an inspiration, as a breath is being taken, the right crus contracts and forces the blood from the inferior cava to the right auricle, an increased supply of blood being thus sent to the right side of the heart at the commencement of each inspiration.   At the same time the crus exerts its force on the left auricle through the dorsal
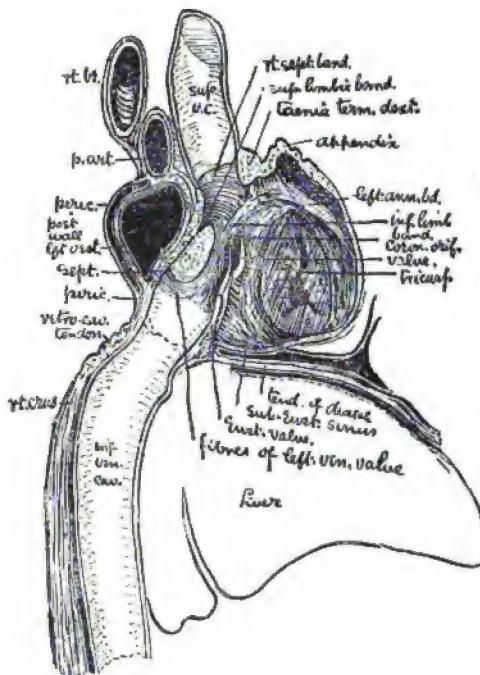
F𝐈𝐆. 7.—Vertical section of the venæ cavæ and right auricle viewed from the right lateral aspect.   It shows the termination of the right crus in the inferior vena cava and base of the heart. Also the muscular bands round the fossa ovalis.

wall of the pericardium.   Traction on the pericardium from below has two effects : it tends to empty the left auricle, and at the same time, by the traction it exerts on the termination of the pulmonary veins, tends to close them.   Thus, during the phase of inspiration, the action of the crus assists increasing the supply of venous blood to the lungs and in decreasing the outflow to the left auricle.   During expiration, on the other hand, its effect is quite the reverse.

The structures which close the venous orifices of the right auricle.— It is now possible for me, with some hope of making my description intelligible, to give an account of how the venous orifices and the

vestibule (that part of the right auricle derived from the sinus venosus) come to be shut off from the auricular *atrium*, or proper auricle, at the commencement of each auricular systole.   Four muscular bands
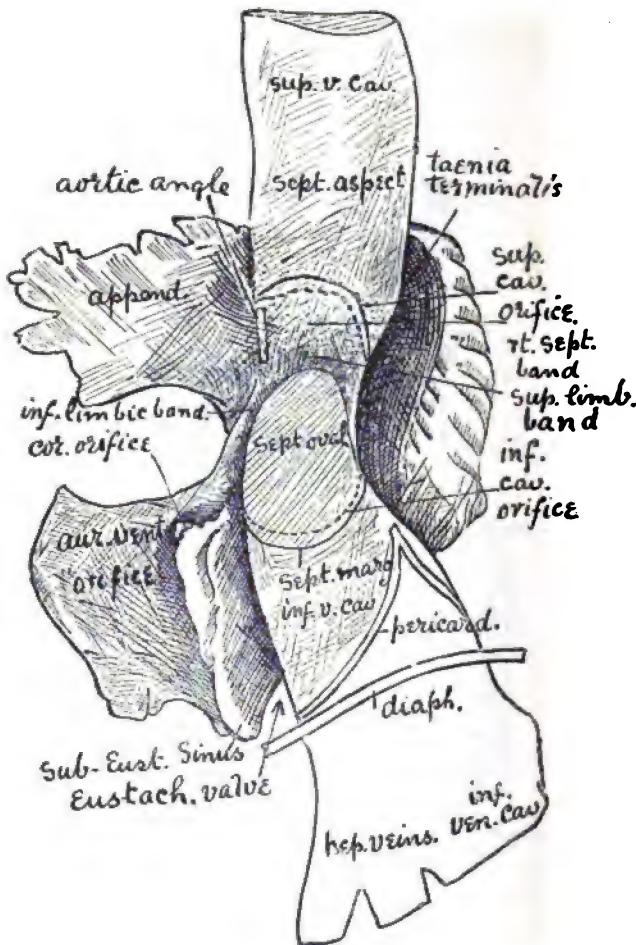
Fig. 8.—Cast of a child's right auricle viewed on its dorsal aspect.   The position
of the aortic angle and certain muscular bands is shown (from the preparation
shown in fig. 1).

bring about this effect—they are present in all mammalian hearts. They are—

   1. The tænia terminalis (figs. 1 and 4).
   2. The inferior limbic band (inferior limb of the annulus ovalis)
      (fig. 9).

3. The superior limbic band (superior limb of the annulus ovalis) (fig. 9).
4. The *septal band* of the right auricle—auricular fibres in the septal wall of the superior caval orifice.

1. *The tænia terminalis.*—This is by far the chief factor in closing the right venous orifices. It is shown in fig. 4, and its position is indicated on the casts of the right auricle shown in figs. 1 and 8. It commences at the mesial fornix of the superior caval orifice, fusing with the musculature of the aortic angle (fig. 2). Passing along the *Eustachian* or anterior margin of the superior caval orifice and the anterior margin of the sulcus terminalis, it terminates below, near the lateral fornix of the inferior caval orifice (fig. 9), by fasciculi which end in the Eustachian fold or valve, and also in other fasciculi which form the lower of the series of the musculi pectinati. By these it is attached to the middle point of the dorsal margin of the right auriculo-ventricular orifice. The musculi pectinati are given off from the left margin of the tænia terminalis (fig. 9), but the musculi pectinati have only an indirect action, which will be alluded to presently, in closing the inferior caval orifice. It is essential to note, in order that the action of the right tænia terminalis may be appreciated, that there is a corresponding band in the left auricle—the *tænia terminalis sinistra.* The left band also starts from the aortic angle and sweeps round the vestibule of the left auricle (fig. 13). That the aortic angle may be identified on the inner aspect of the right auricle, it may be mentioned that the convexity of the annulus ovalis is embedded in it. In the auricular systole both contract together, the one tænia acting as an opponent to the other. When the right tænia terminalis contracts, it descends within the right auricle like the blade of a falchion (fig. 9). The anterior or Eustachian margin of the superior caval orifice is brought downwards and inwards until it approaches the aortic wall of the right auricle, just in front of the aortic auricular angle (figs. 2 and 9). The lateral fornix of the inferior caval orifice is the only point at which the tænia terminalis is absolutely fixed (fig. 6). Hence, when this band contracts, the mesial or left fornix of the superior caval orifice is drawn towards the lateral fornix of the inferior caval orifice (figs. 1, 8, 9).

2. *The inferior limbic·band.*—This band is really, in nature, a *musculus papillaris.* It might be described as the *tensor valvulæ Eustachii,* but such a term does not describe its action fully. It is attached to the Eustachian valve and inner or mesial fornix of the inferior caval orifice (figs. 4, 7, 9). From that origin it passes to its insertion on the central fibro-cartilage of the heart (see figs. 7, 9 and 10). The band acts in two ways: it lifts up and renders tense the Eustachian valve along the anterior or Eustachian margin of the inferior caval orifice, and at the same time brings the bases of the ventricular orifices towards inferior caval orifice—thus assisting to close the vestibule of the right auricle (figs. 1 and 9).

It will be observed that the mesial extremity of the Eustachian

valve is attached to the inferior limbic band, its lateral extremity to the tænia terminalis (fig. 4). These two bands practically encircle the auricle and separate its vestibule from its atrium (figs. 1, 8). It must be remembered, however, although the Eustachian valve is made tense and stretched so as to bring it somewhat towards the septal margin of the inferior caval orifice, that it is the aortic auricular angle (fig. 2) and the central fibro-cartilage of the heart (fig. 10) that are the movable points, and these are brought towards the inferior caval orifice (fig. 9).
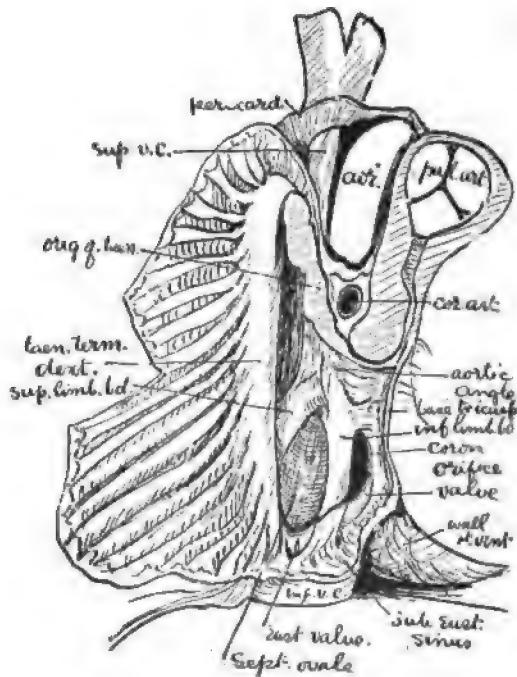
Fig. 9.—The right auricle of a child's heart, which was thrown into a partial contraction by the injection of hot wax, opened and view from the front. The anterior wall is thrown to the right; the right tænia terminalis is pulled upwards and to the right to show the parts which it covered. It was in contact with the interior limbic band.

The Eustachian valve.—This valve forms the anterior, right or Eustachian margin of the inferior caval orifice (fig. 7). It is never absent in the normal human heart. It is only absent when destroyed by the effects of disease. The denial of its presence is the result of a failure to distinguish between this valve and the right venous valve of the sinus venosus. The Eustachian valve, it is true, is part of the right valve of the sinus venosus, but it is derived from only the *basal*

part of that segment of the right venous valve which forms the anterior margin of the inferior caval orifice. The free, non-muscular part of this segment of the right venous valve is fretted and forms a thin network, and disappears at birth or soon after. But the basal part which forms the Eustachian valve is always present. The membranous part of the right venous valve which skirts the anterior or Eustachian margin of. the superior caval orifice disappears, but its position can be distinguished (fig. 4).

The sub-Eustachian sinus.—This is the Valsalval sinus of the inferior caval orifice, and it is not only present in all mammalian hearts, but can also be seen in the reptilian auricle (figs. 1, 3, 4, 5, 7, 8). It is formed by that part of the atrium of the right auricle which lies between the Eustachian valve and left margin of the orifice of the
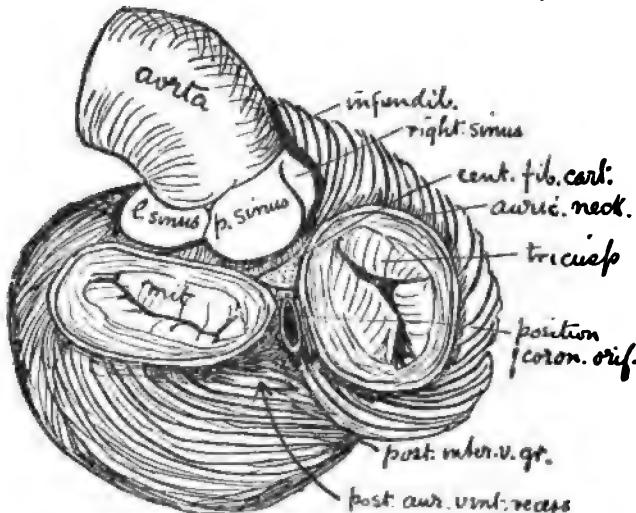
FIG. 10.—Preparation to show the relationship of the central fibro-cartilage to the posterior cusp of the aorta, to the auriculo-ventricular orifices, and to the opening of the coronary sinus.

right ventricle. There the auricular wall is extremely thin and only slightly muscular. It is in reality an interval between the lowest of the musculi pectinati and the muscular fibres of the tænia terminalis that end on the lateral fornix and Eustachian margin of the inferior caval orifice (figs. 1, 4, 8). When the *musculi pectinati*, by which the wall of the atrium is formed, begin to contract, the sub-Eustachian sinus is unduly distended by the tension thus raised in the atrium. The Eustachian or free part of the anterior margin of the inferior caval orifice (fig. 7) is pressed backwards by the distending sinus until it is firmly applied to the septal wall (figs. 9, 15).

3. *The superior limbic band.*—The action of the superior limbic

band (superior limb of the annulus ovalis) in closing the vestibule and venous orifices of the right auricle, can be seen by referring to figs. 9 and 11. It takes its fixed origin from the lateral fornix of the inferior caval orifice, from the sulcus terminalis just above that fornix, and by a series of fibres (see fig. 5) from the left or septal margin of that orifice. From those points of origin the band passes on the right aspect of the interauricular septum to terminate in the aortic auricular angle (fig. 2), and some of its fibres join those of the inferior limbic band.

At the commencement of an auricular systole, this band draws back the aortic angle of the auricles, and consequently the base of the right ventricle towards the lateral fornix of the inferior caval orifice (fig. 15). It thus assists in emptying the vestibule of the right auricle, ˙and coming against the tænia terminalis, shuts the vestibule off from the atrium (fig. 9).

4. *The auricular fibres at the septal margin of the superior caval orifices* (figs. 7 and 11).—This is the fourth and last of the bands of muscular fibres which have to be considered in connection with the closure of the caval orifices of the right auricle (figs. 7 and 8). The fibres of this flat band rise from the fibrous tissue of the *sulcus terminalis* (fig. 11), and proceed backwards in the auricular septum and septal wall of the superior caval orifice to terminate in (*a*) the aortic angle (figs. 2 and 11), (*b*) the tænia terminalis sinistra (fig. 11). Their main function is to draw backwards the aortic angle and ventricular bases, and thus empty the vestibule of the right auricle. At the same time, this bundle becomes approximated to the tænia terminalis, thus occluding the superior caval orifice (figs. 2, 15).

Tubercle of Lower.—It is this muscular band that gives rise to the tubercle of Lower. The tubercle is well marked in all pronograde mammals. In these the superior and inferior caval enter the vestibule of the right auricle at an angle to each other, which is about 100° in extent. In orthograde mammals, the anthropoids and man, the venæ cavæ are more nearly in a line, and open at an angle to each other of about 140°. Thus in pronograde mammals there is a distinct angle at the junction of the cavæ in the septal wall, below and to the right of the superior caval orifice; in that angle is the septal band of muscle just described. To apply the term tubercle to a band of muscle is a misuse of terms, but it would be extremely convenient to retain the term as *the angle of Lower*, so that one could indicate the degree of inclination of the superior cava to the inferior cava ˙as these vessels entered the vestibule of the right auricle.

Using the term as above defined, it may be said that the angle of Lower in the human fœtus at and before birth is ˙of only slightly greater extent than the corresponding one in pronograde mammals.

Loop-shaped fibres at the termination of the superior vena cava (fig. 13).—The terminal half-inch of the superior vena cava is surrounded by loops of muscular fibres. The convexities of the loops are thrown round the mesial or left margin of the superior vena and terminate at the right or lateral margin near the lateral fornix of the

vein (figs. 8 and 11).   They assist in constricting the terminal part of the vein and assist the tænia terminalis.   These fibres I regard as the only representative of the musculature of the sinus venosus now remaining in the mammalian heart.   All the other bands that help to close the orifices are derived from the auricle.   It is probable that the contraction of the vestibular systole is initiated in the loop fibres of the vena cava.
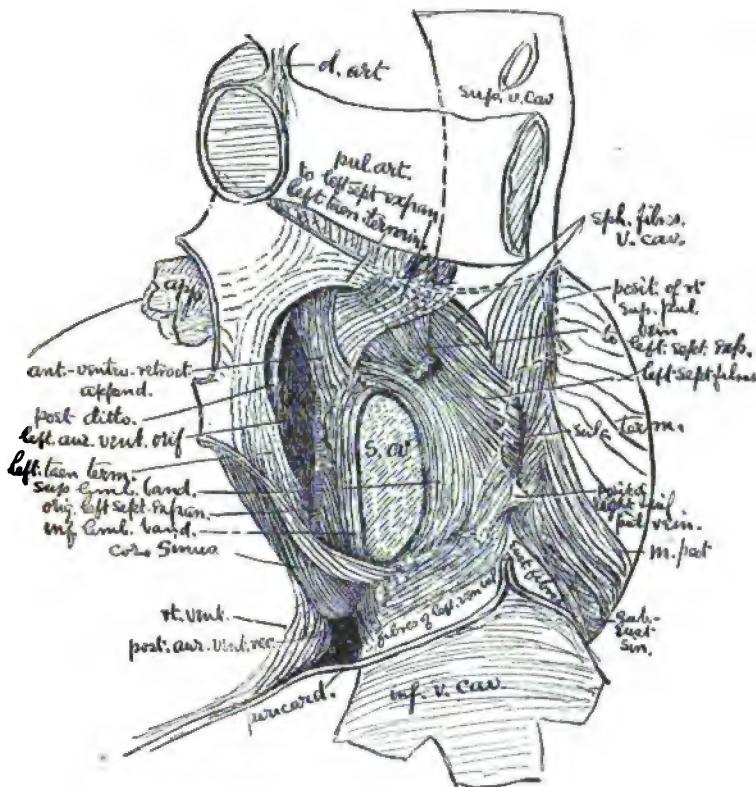
Fig. 11.—The foramen ovale—the oval space between the limbs of the annulus ovalis—exposed from behind by removing (1) the posterior wall of the left vestibule, (2) the fibres of the interauricular septum belonging to the left vestibule.   Owing to an attempt to leave an outline of the right pulmonary veins, the arrangement of the septal fibres appears somewhat involved.

The coronary orifice.—The closure of the coronary orifice can be briefly described.   The anterior or Eustachian margin is formed by a fold which is derived from the lower or ventricular extremity of the right venous valve (see figs. 14, 19, 20).   The septal margin is formed by the mesial or ventricular extremity of the inferior limbic band (fig. 4).   This band is developed in the base of the mesial

(ventricular) extremity of the left venous valve and in the fold of the sinus venosus which separates the right and left horns of that cavity (see fig. 14).

The contraction of the inferior limbic band brings the septal margin of the orifice against the valvular fold on the Eustachian margin.

The valvular mechanism of this orifice frequently breaks down in cases of venous back pressure.   It is the next to fail after that of the inferior cava, and I suspect that many of the unexplained symptoms of heart disease are due to the hypertrophied right auricle pumping its
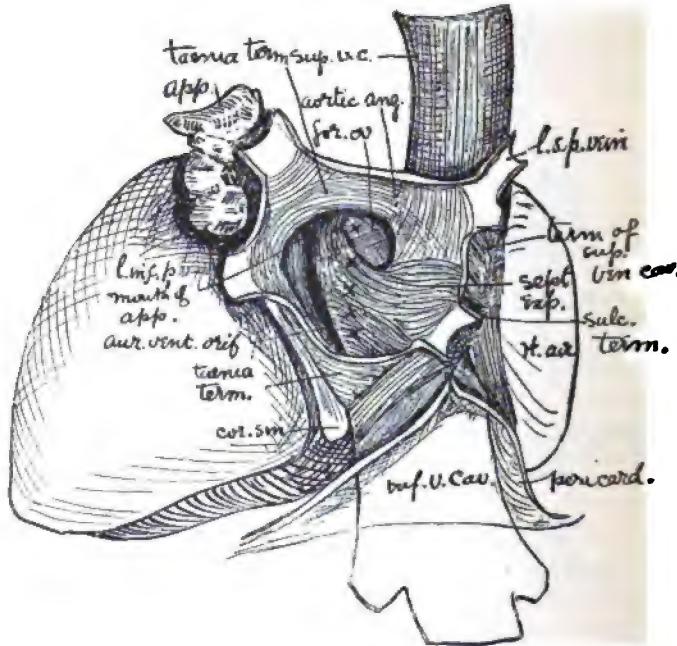
FIG. 12.—Left tænia terminalis and anterior wall of the vestibule of the left auricle.   They are exposed by the removal of the posterior wall of the vestibule.   The crosses mark the line along the base of the septum with which the left tænia terminalis comes into contact in systole of the auricle.

blood into the coronary sinus and veins of the walls of its own heart. The valves at the terminations of the cardiac veins in the coronary sinus are not strong enough to resist such a persistent force as that of the hypertrophied right auricle.

It will be seen that when the tænia terminalis sinks within the auricle, and when the superior limbic band contracts and pulls back wards the aortic angle of the auricle, that the convexity of the superior limbic band fits accurately within the concave margin of the tænia terminalis (fig. 9).   The more these bands contract the firmer they are locked in each other's embrace, so that it is impossible that there

could be a regurgitation of the blood in the atrium into the vestibule or superior venæ cavæ. The firm application of the Eustachian margin of the inferior caval orifice to the septal wall forms a competent valvular mechanism, and as long as this margin remains intact, there can be no regurgitation of blood to the inferior cava.

Remnants of the left venous valve of the sinus venosus and of its musculature.—In order that the septal margin of the inferior caval orifice may be straightened and become a firm basis against which the Eustachian margin may come in firm and uniform contact, a band of muscle is present. This passes along the septal margin of the orifice, commencing in the inferior limbic band (fig. 7), and ends in the superior limbic band (fig. 11). It is a remnant of the musculature of the left venous valve. It skirts the septal margins of both the superior and inferior caval orifices and assists in bringing their margins together (fig. 11).

It is usually said that there is no trace of the left valve of the sinus venosus to be seen in the fully formed human heart. On the contrary, two very distinct remnants can always be seen on the septal margins of the two caval orifices. That at the inferior caval orifice forms fibrous reticulations along the base of the septum ovale (fig. 4). On the septal wall of the superior caval orifice it forms the valvular fold of the endocardium which covers and protects the mouth of the septal vein of the auricles (fig. 4).

The occlusion of the vestibule and venous orifices of the left auricle.— The manner in which the vestibule and venous orifices of the left auricle are shut at the commencement of an auricular systole will be best understood by referring to figs. 5, 12 and 13. Three parts of the musculature of the left auricle are employed to attain this end. They are—

1. The tænia terminalis sinistra.
2. The left septal expansion or band.
3. The semicircular bands surrounding the venous orifices.

1. *The tænia terminalis sinistra.*—Just as in the case of the right auricle, but to a more marked extent in the case of the left, this strong muscular band, when it contracts, separates the vestibule of the left auricle from the cavities of the atrium and appendix. Not only is it similar to the right tænia in function, and almost in attachments, but it is also identical in the manner in which it is developed (see p. xxxiii).

The tænia forms an almost complete circle, as complete as the external semilunar cartilage of the knee-joint, which it somewhat resembles (fig. 12). Its anterior or ventral extremity starts in the aortic angle of the auricle; there it fuses with the corresponding tænia of the right side and with the septal band of the superior caval orifice (see figs. 2, 11 and 13). The posterior or dorsal extremity has a rather extensive attachment (figs. 11 and 12). Some of its fibres reach the

central fibro-cartilage of the heart, others end in the septal margin of the inferior vena cava and left margin of the left auriculo-ventricular orifice (figs. 11 and 12.)

In fig. 11 the left auricle is represented in a state of partial contraction. The tænia terminalis has become drawn within the cavity of the left auricle. Its free crescentic edge is directed towards and ultimately comes into close contact with the base or ventricular margin of the septum ovale. It is similar in origin, nature and action to the opponent band of the right side. It shuts off the vestibule of the left auricle from the atrium.

The left septal expansion (figs. 5 and 11).—This muscular expansion corresponds in position, action and origin to the superior limbic band
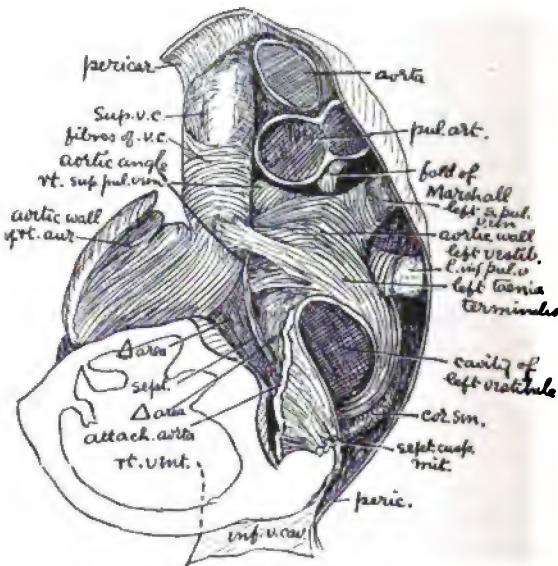
FIG. 13.—The aortic angle and aortic walls of the auricles exposed by removing the aorta, left ventricle, and the greater part of the right. The origin of the left tænia terminalis is shown. The appendix of the left auricle is also removed. The thin triangular area on each side of the septum is indicated.

and septal fibres of the superior caval orifice of the right auricle (see figs. 11, 17, 7). The fibres arise chiefly from the superior marginal attachment of the left auricle, but also from the right and left marginal attachments of the left vestibule (fig. 5). These points are fixed. The fibres enter the septum of the heart and terminate in the right margin of the left auriculo-ventricular orifice—in the dorsal half of that margin (see fig. 11). Its insertion will be seen to lie within the concavity of the crescentic margin of the tænia terminalis (fig. 12). When contracted they lock upon each other.

It can now be seen how the tænia semicircularis and septal band

shut the vestibule of the left auricle completely off from its atrium. The vestibule has only two walls, a posterior or dorsal, formed chiefly by the left septal expansion (fig. 5), and a ventral or anterior (fig. 12), formed (1) by the inter-auricular septum, and (2) by the left tænia terminalis (fig. 15). The combined action of the left tænia terminalis and left septal expansion is such that the anterior or septal wall is pressed firmly against the posterior wall. The communication of the vestibule with the atrium is firmly shut, owing to the manner in which these two bands are locked, the septal band expansion hooking round the concavity of the crescentic tænia terminalis (fig. 12).
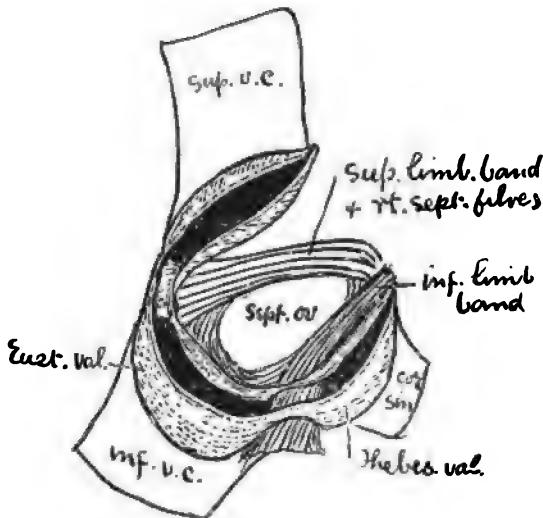
FIG. 14.—Showing how the orifice of the right sinus venosus is subdivided into three by two infoldings of the sinus wall. In the infolding between the coronary and inferior caval openings lies the inferior limbic band; in that between the caval openings, the right septal fibres and the superior limbic band. The right and left venous valves are represented.

The looped fibres of the pulmonary orifices.—To make doubly sure, as it were, that the auricular contraction cannot spread backwards to the veins of the lungs, looped fibres are placed at the pulmonary orifices (fig. 5).

Retraction of the ventricles during the auricular systole.—It is a fact clearly recognised by physiologists that the ventricles are drawn backwards on the load of blood within the auricles, much in the same way as a stocking is drawn on the leg. The ventricular base is drawn towards the fixed points of the heart already described (fig. 6). In this movement the auricular septal fibres certainly play a part, but these fibres draw the base of the heart not only backwards but also towards the inferior caval orifice. The septal fibres only act on a

limited part of the base of the ventricles, the part shown in fig. 12 During the auricular systole each auriculo-ventricular orifice forms a narrow ellipse; each has a lateral and a mesial margin. Only the dorsal parts of the mesial margins come into contact (fig. 12). At that part the margins are fused with the interauricular septum (fig. 15). It is only this part of the ventricular base that is retracted by the septal fibres. The remainder of the base of the ventricles is retracted by the contracting fibres of the auricles proper.

The manner in which the foramen ovale and ductus arteriosus are closed at birth.—In fig. 16 is shown mesial section of the thorax of a child at birth. The section which is represented does not show well the high position of the lungs and heart, the tortuous course of the œsophagus, or the wavy course of the phrenic nerve at birth. All are huddled in the upper region of the thorax, waiting the first movement of the diaphragm to bring them into position.

The heart beats under very different circumstances before birth. The fixed points from which it acts are different. It works under the same circumstances as does the heart of the bird all through life. There are no respiratory movements to disturb its action. Most important of all, the heart is not moved by the right crus of the diaphragm. It is the action of this muscle at birth which upsets the principles on which the fœtal circulation is conducted.

The action of the superior and inferior limbic bands before birth.— The fixed points from which these bands act during post-natal life are the mesial and lateral fornices, but especially the lateral fornix of the inferior caval orifice. These two points are moved and controlled by the traction of the right crus of the diaphragm. But in pre-natal life, the crus being non-operative, these two bands pull the fornices of the inferior caval orifice within the vestibular chamber to quite as great an extent as they draw the aortic angle backwards. Indeed the latter must be by far the more fixed point, for the heart is surrounded by the solid unyielding lungs. It is extremely probable that the limbic bands actually pull on the right crus. By this means they force the blood in the inferior vena cava within the chamber of the right auricle. The right crus certainly acts as a respiratory pump after birth, and in the manner indicated it may also serve to feed the heart before birth.

The manner in which the limbic bands act in pre-natal life prevent them from completely occluding the vestibule from the atrium of the right auricle. Hence, when the right auricle contracts, it forces the blood in two directions—into the right ventricle, and also through a narrow chink of the foramen ovale into the left auricle. Blood may also pass through the foramen ovale into the left auricle before the commencement of the auricular systole. The foramen ovale is an adaptation to secure an equal pressure in both auricles, and therefore an equal supply of blood, during auricular systole.

At birth the contraction of the diaphragm—which then descends downwards and forwards to the extent of about one inch—completely alters the action of the limbic bands. Their fixed points are now

defined, and when they and the tænia terminalis contract, the vestibule of the right auricle, and of course the fossa ovalis, are completely shut off from the atrium.

Closure of the ductus arteriosus.—By the contraction of the right crus the ductus arteriosus is also closed. The manner in which this is accomplished may be seen from fig. 16. The tendon of the crus is prolonged by the dorsal wall of the fibrous pericardium to the fixed
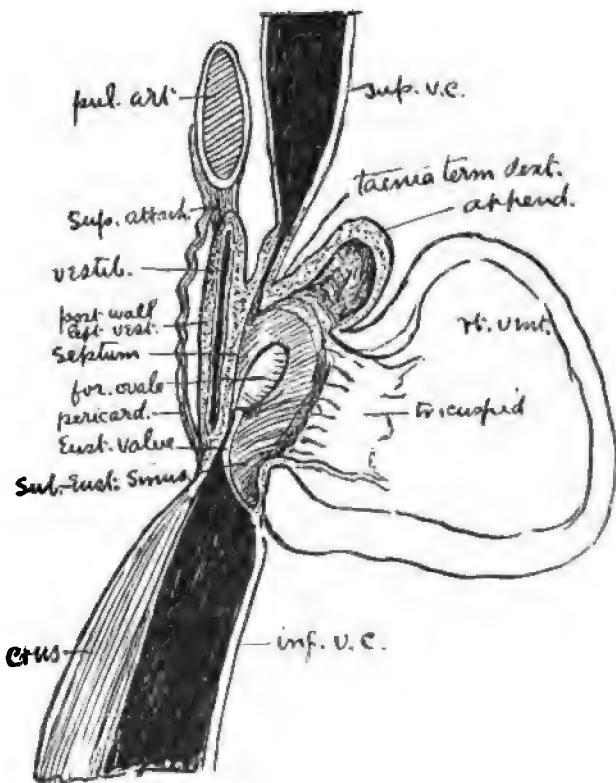
Fig. 15.—Diagram to show the occlusion of the left vestibule, the closure of the venæ cavæ, and retraction of the bases of the ventricles as the auricles are emptied.

margins of the left auricle (see fig. 15). At the junction of the superior and left marginal attachments, just where the left superior pulmonary artery emerges from the root of the lung, lies the ductus arteriosus. To it is attached the superior left extremity of the dorsal part of the pericardium (fig. 6). When the right crus contracts at birth, with the first inspiration, it draws the pulmonary arteries and the fixed margins of the vestibule of the left auricle with it, but the aorta is fixed otherwise and scarcely yields. Hence a decided traction is exercised on the
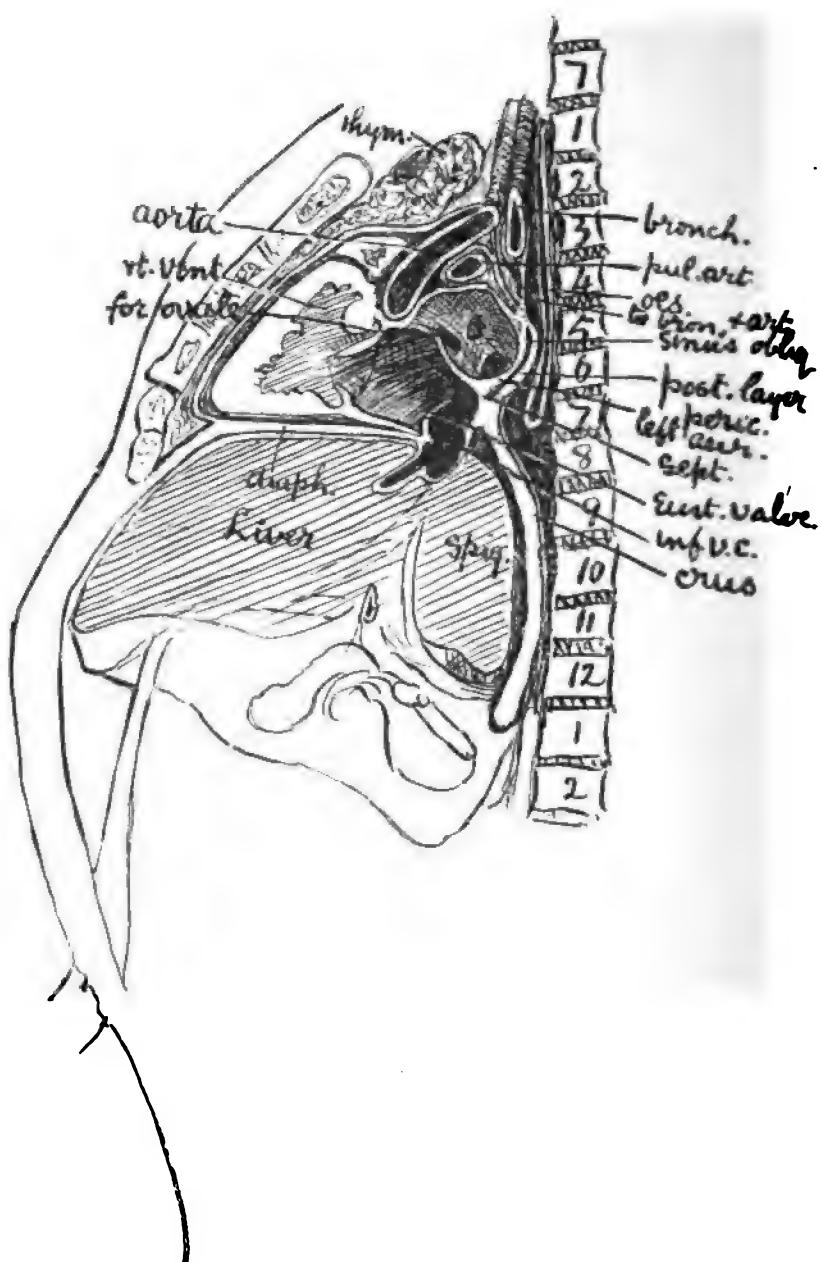
FIG. 16.—Vertical coronal section of the thorax of a still-born child, to show the termina-
tion of the right crus in the inferior vena cava, septum of auricles, posterior layer of
pericardium, and in sheaths of pulmonary arteries and bronchi.

ductus arteriosus—enough I believe to stop the flow of blood from the pulmonary artery to the aorta and turn it into the lung, which at the same moment is expanding.

Thus the contraction of the right crus, while helping to expand the lung, also closes the foramen ovale and ductus arteriosus.
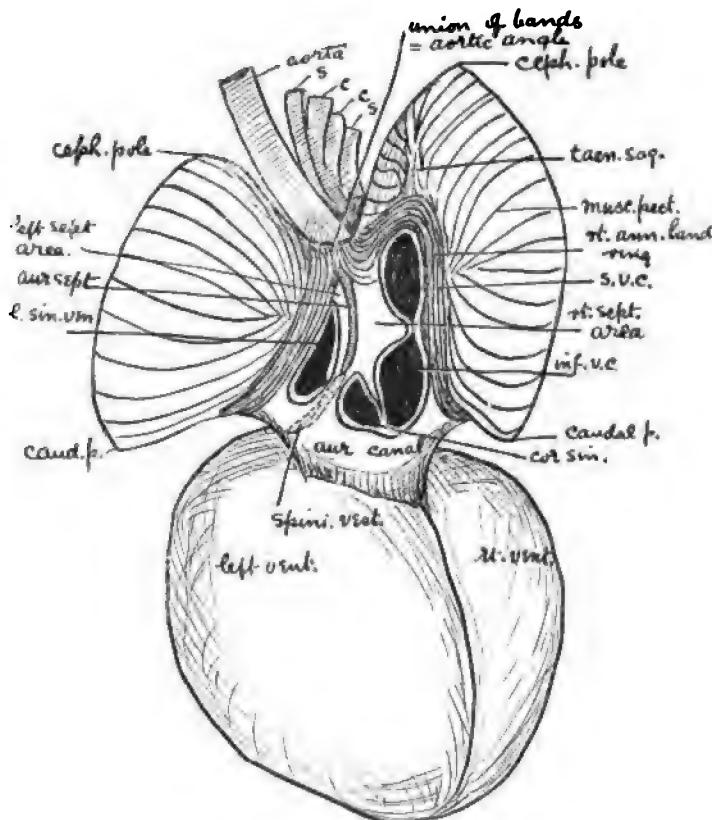
FIG. 17.—The dorsal aspect of the auricular part of an abnormal (reptilian-like) human heart. The venous openings are shown on the dorsal aspect of the primitive auricular canal (auricular segment of primitive cardiac tube). The septal (or intersinuous) areas, the annular (basal) bands of the auricles, the caudal and cephalic poles, and the primitive arrangement of the musculi pectinati are also represented.

The morphology of the auricles.—An investigation into the morphology and development of the auricles shows that the various structures which close the vestibules of the auricles from the atria serve identical functions, although they differ in form, in the reptilian,

avian and mammalian heart. The same elements are present in all three kinds of hearts; they serve the same function in all; they only differ in the manner of their combination.

The right and left sinus venosus.—In fig. 17 I have diagrammatised the dorsal aspect of the auricles of a heart which was obtained from a human child, but which resembles in every detail the reptilian heart. The points to be noted are—

1. The right sinus venosus receives the superior cava, inferior cava and coronary sinus; but, as can be seen from fig. 20, a fold of the sinus projects within the cavity of the auricle and separates the orifice of the sinus venosus into two.

2. The right sinus venosus does not open into the auricle proper, but into that part of the cardiac tube which I shall indicate as the auricular segment of the cardiac tube.

3. The left sinus venosus receives the two pulmonary veins, and also opens into the auricular segment of the primitive cardiac tube. It is separated from the right sinus by an inflection, similar to that which we have seen to separate the coronary from the caval openings. To this inflection— the *intersinuous fold*—I will have to refer to again. A reference to comparative anatomy shows that the two sinuses are originally one.

4. From the dorso-lateral aspect of each side of the primitive cardiac tube the two auricles have been developed as hollow outgrowths. On the dorsal aspect of the tube their bases meet; on the ventral aspect of the tube they do not meet, but leave a narrow tract of the auricular segment of the cardiac tube.

5. The mouth or base of each auricle is surrounded by a ring of muscle—the *basal ring* of muscle. On the dorsal aspect of the cardiac tube, where the bases of the auricles are in contact, these rings fuse, elsewhere they are free. From these rings are developed the valvular venous mechanism of the fully formed heart.

6. Muscular fibres pass elliptically from the *lateral* segment of each basal ring, round the auricle, to end in the *mesial* segment of the ring. They come to form the musculi pectinati. They are derived from the basal rings during the growth and expansion of the auricles.

The relationship of the auricular to the ventricular segment of the primitive cardiac tube.—By an arrest of growth during development, the terminal part of the auricular tube comes in contact with the terminal part of the ventricular segment, so that the right margin of the base of the aorta remains in juxtaposition with the auricle; unless this point is grasped, the development of the cardiac septa cannot be understood (see fig. 18).

It will be seen by referring to fig. 18 that at three points the primitive cardiac tube remains during development in a condition of passivity. The first and most important is on the right dorso-lateral aspect of the primitive cardiac tube where the auricular and ventricular segments unite. This union forms the right margin of the right auriculo-ventricular orifice in the reptilian heart (fig. 19) and also in the abnormal human heart (fig. 20). Its destination is so

important that a name must be given it—provisionally it may be termed the *right auriculo-aortic angle* (fig. 18). In the fully formed human heart it becomes fused in the central fibro-cartilage of the heart.

The second point at which the cardiac tube remains stationary is along a spiral line on the left aspect of the ventricular part of the cardiac tube. This line forms the upper margin of the interventricular septum. The left ventricle is developed as an evagination from the ventricular segment to the left side of this line. It grows backwards and to the left, giving the ventricular fibres the curious spiral twist they possess. The right ventricle is produced as an evagination on the right side of this line, its growth being forwards (ventralwards) and to the right. The rounded opening between the upper margin
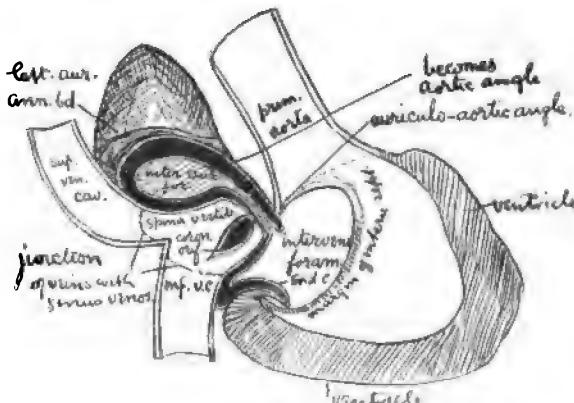
FIG. 18.—A diagram to show the parts of the cardiac tube which remain almost stationary during the development of the heart. The chief stationary point is on the dorsal aspect of the ventricular part of the tube ; here the auricle practically joins the aorta. The other is on the ventral aspect of the auricular part of the tube ; here the sinus venosus practically joins the ventricle. The parts of the tube formed by the sinus venosus and aorta (truncus arteriosus) are represented in outline : the part by the auricle, black ; the part by the ventricle, shaded.

of the interventricular septum and auriculo-ventricular angle constitutes the true interventricular orifice, and represents an arrested ring of the primitive cardiac tube (fig. 18).

The third point of the primitive cardiac tube to remain in abeyance is the ventral margin of the auricular segment of the cardiac tube (fig. 18).

A consideration of these points shows how it is that on the ventral aspect the sinus venosus comes almost in contact with the ventricles, and the distal end of the auricular tube with the distal end of the ventricular.

The morphology and development of the septum ovale.—The septum ovale is primarily the right valve of the left sinus venosus. That purpose it serves in the reptilian heart; it serves so in the human

heart (fig. 20); it also serves as such in the human fœtal heart until the time of birth, and after birth it assists to close the vestibule of the left auricle—a derivative of the left sinus venosus. It acts only as the right valve; the basal muscular ring of the primitive auricle brings the left orifice of the sinus against the septum ovale. The left tænia terminalis is a derivative of this ring and acts in similar manner in the fully formed heart.
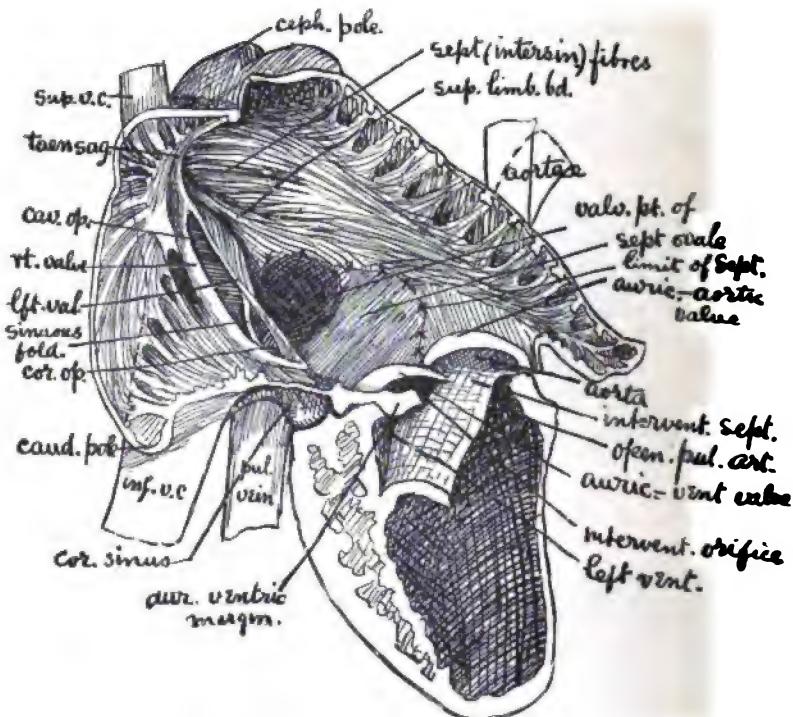
FIG. 19.—The heart of a python laid open and viewed from the right lateral aspect. The septum ovale (non-muscular) constitutes the whole of the real interauricular septum, only the posterior (deeply shaded) part acts as a pulmonary valve. The right auriculo-ventricular orifice is thrown open; it is bounded on the right by the auriculo-aortic valve, the representative of part of the anterior endocardial cushion; on the left by another valve, which represents part of the posterior endocardial cushion.

Development of the septum ovale.—The septum ovale is developed by the combination of two elements, but by far the chief one is that described by His as the spina vestibuli. This is an outgrowth from the intersinuous fold, or what His has named the area interposita (see fig. 22). The area interposita is really the forming mouth of the left venous sinus; it is from the right margin of this area that the

spina vestibuli springs. The second element in the septum ovale is the true interauricular septum—that septum which is formed on the dorsal aspect of the primitive cardiac tube between the bases of the auricular outgrowths. At its proximal or cephalic end it is continuous with the spina vestibuli. The spina vestibuli, starting from
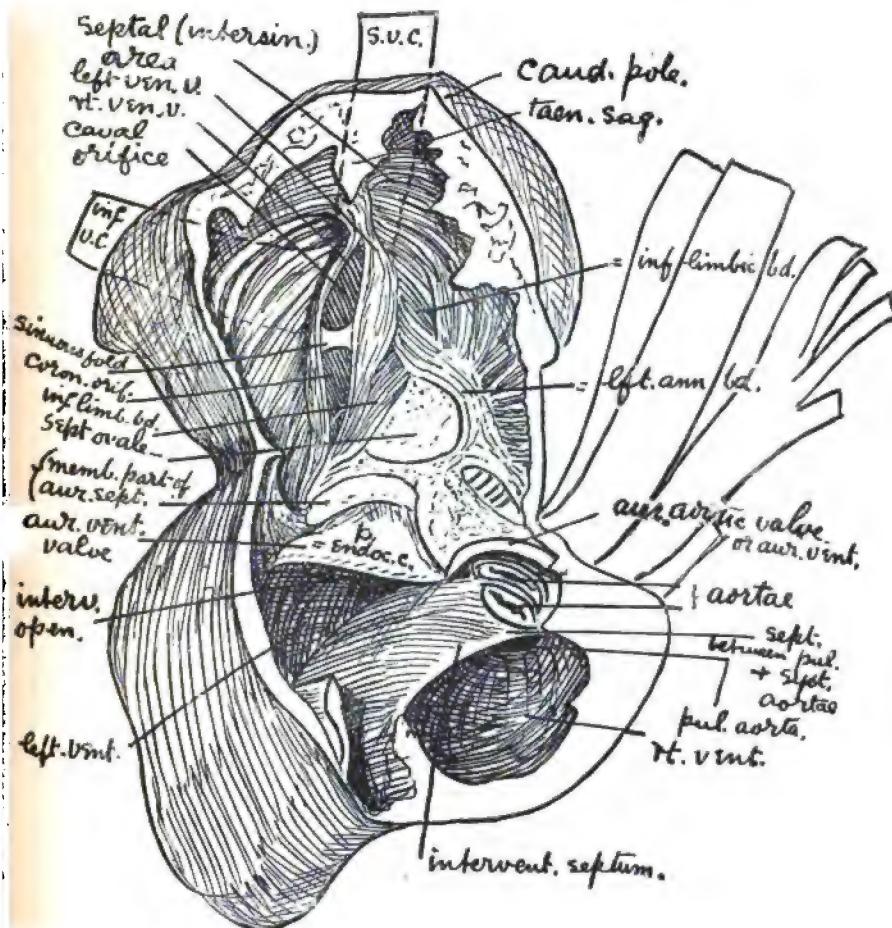
FIG. 20.—An abnormal human heart thrown open. It shows all the characters of the reptilian heart.

the inter-sinuous fold, grows forwards, as a triangular fold, until it comes in contact with the auriculo-aortic angle, with which its point and concave margin fuse (fig. 18). Thus the auricles are completely separated. The interauricular septum of the reptilian heart, and of the human heart shown in fig. 20, is formed entirely by the

septum ovale.   To this septum Born gave the name of septum primum, and it represents the septum superius and spina vestibuli of His.

Development of the inferior limbic band.—It will be remembered that the inferior limbic band is attached to the central fibro-cartilage of the heart (fig 10).   That mass of fibrous tissue is developed in the auriculo-aortic angle (fig. 18).   When the spina vestibuli grows forwards (fig. 23) it carries with it three sets of auricular fibres: (1) those at the base of the left venous valve, (2) those in the left *inter-sinuous* area (fig. 17), (3) some fibres of the left annular ring of the left auricle.   The fibres carried forwards from the left venous valve afterwards form the inferior limbic band; they lie in part in the fold between the coronary and caval orifices of the sinus (figs. 19 and 20).   The fibres carried forwards from the left intersinuous area form the septal band on the left vestibule.
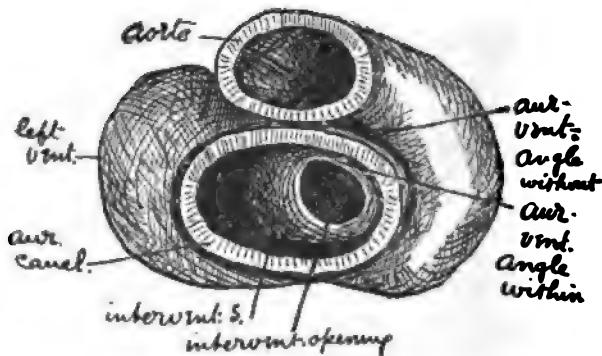
FIG. 21.—Diagram prepared from His's model of the ventricular segment of the heart at about the third week of development.   Through the auricular canal is seen the interventricular foramen.   The foramen represents a ring at which growth has been nearly stationary.   It is bound on the left and ventral aspect by the margin of the interventricular septum ; on the right by the auriculo-ventricular or *auriculo-aortic* angle.   On the margin of the opening opposite to the septum are developed the central fibro-cartilage and anterior endocardial cushion.

The vestibule of the left auricle.—This is developed entirely, if one includes the septum ovale, from the left sinus venosus.   The expansion of the sinus and its migration to the left is attended by four circumstances which can be understood by comparing figs. 17, 11 and 5.

1. The dorsal or right segment of the annular basal band is carried to the left before the sinus, and forms the left tænia terminalis.

2. The septal band is pulled outwards and to the left to cover the posterior or dorsal wall of the vestibule.

3. The left duct of Cuvier is also pulled to the left, so that it surrounds the vestibule.

4. The migration outward and development of the sinus into the vestibule leads to a rupture of the attachment of the septum ovale to the aortic wall of the auricle.   This break-down occurs at the part

where the crescentic margin of the septum ovale (septum primum) fused with the wall of the auricle. *By this rupture* is formed the fora-men ovale, which, as Born has shown, is formed by a breaking down of the septum primum.

The superior limbic band and septal fibres of the superior caval orifice.—These are developed from the intersinuous fibres of the right auricle (fig. 17). Some of them, too, are derived, in a way I shall show, from the fibres of the muscular ring of the right auricle and from the left segment of that ring. Their nature can be best under-stood by a reference to figs. 19 and 20. In these two hearts it will be seen that those fibres pass from the upper half of the base of the left venous valve to the margin of the septum ovale, but many pass into the left segment of the annular band. All these fibres formed at first part of the annular band, and terminated by joining the right segment of the band (right tænia terminalis) at the upper (cephalic)
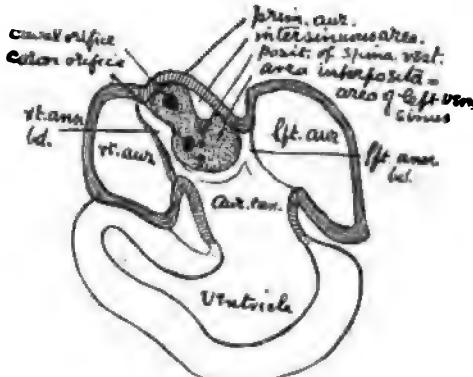
FIG. 22.—An interpretation of the figure given by His of the interior of the heart of a human embryo about 3 weeks old (Embryo Bl).

fornix of the orifice of the right sinus venosus. The migration upwards of the sinus on the posterior wall of the auricle, owing to the descent of the heart, has led to the spreading out of these fibres along the base of the left venous valve.

His, quite rightly, does not mention the annulus ovalis (made up of the superior and inferior limbic bands) as forming any part of the septum of the heart. Born describes its formation from what he has termed the septum secundum. But it will be seen that the inferior limbic band is part of the septum primum, and the superior limbic band is part of the right annular band.

The annular bands of the primitive auricles.—These muscular rings have been already alluded to, and are shown in fig. 17. Each ring is elliptical, and made up of a lateral and mesial segment. The lateral segment of the right auricle forms the right tænia terminalis; the mesial segment of the left forms the left tænia terminalis. The lateral segment of the left auricle can be seen passing round from the

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aortic angle, between the appendix and ventricle, to end on the left
margin of the left auriculo-ventricular orifice. The mesial segment in
the right auricle can be traced from the aortic angle round the aortic
wall of the right auricle, and terminates in the lowest series of the
musculi pectinati.

The aortic angle.—The aortic angle (figs. 2 and 13) is formed where
the two auricular rings fuse on the dorsal wall of the cardiac tube (fig.
17). From that point the rings diverge. As they pass forwards they
leave on each side of the attachment of the septum ovale a thin
triangular area, which can be recognised in the fully formed heart (fig.
13). These triangular areas lie against the stem of the aorta.
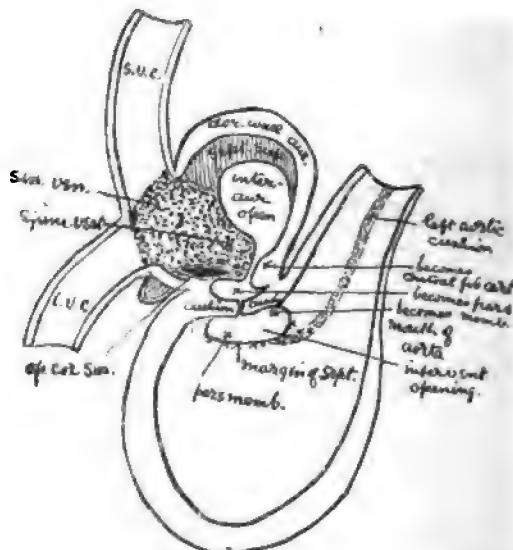
FIG. 28.—Showing the formation of the septum ovale (septum superius and
spini vestibuli of His), septum primum of Born. The main element in its
formation is the spini vestibuli—a development of the sinus venosus. The
endocardial cushions are within the ventricular segment of the cardiac tube.
I have been greatly assisted by the figures given by Dr Alex. Low in the
Proc. of the Aberdeen Univ. Anat. and Anthropol. Soc., 1900-1902.

The nature of the endocardial cushions.—We have seen that the
septum ovale completely divided the auricular segment of the
primitive cardiac tube into right and left halves. The endocardial
cushions are developed entirely in the ventricular segment of the tube.
They are derived, as His has observed, from an infolding at the
auriculo-ventricular junction of the cardiac tube.

The dorsal and ventral endocardial cushions undoubtedly represent
the dorsal and ventral auriculo-ventricular valves of the amphibian
heart. In the reptilian, avian and mammalian heart these two
cushions or valves fuse. The dorsal cushion is constant as regards

its position and relationships in all hearts; but the ventral cushion varies in its position and relationships.

In the reptilian heart the endocardial cushions are fused and are represented by (see figs. 19 and 24) the left auriculo-ventricular valve and the mesial right auriculo-ventricular valve. The left valve prevents the return of the blood to the left auricle. The two valves of the right auriculo-ventricular orifice serve two purposes: (1) they prevent the return of the blood from the common ventricular cavity to the right auricle, and (2) with the interventricular septum form the orifice of the aorta. The right valve of the right auriculo-ventricular orifice of the reptilian heart represents the auriculo-ventricular (aurieulo-aortic) angle (see figs. 21, 23).

The reptilian and mammalian heart differ chiefly in the development of the ventral endocardial cushion. In the reptilian heart it springs from the base of the left ventricle; in the mammalian heart
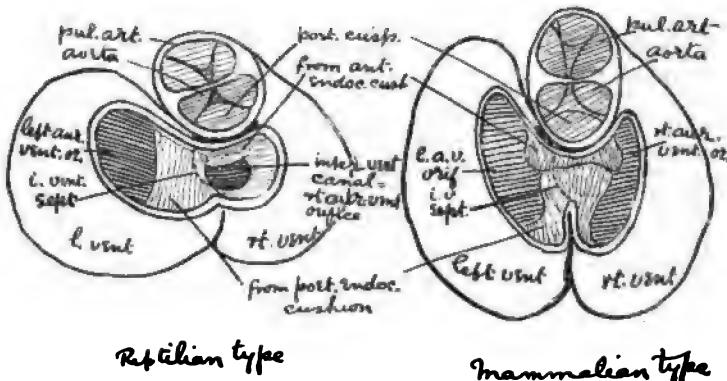

FIG. 24.—Two diagrams to contrast the arrangement of the endocardial cushion s in the reptilian and mammalian hearts.

it arises not only from the base of the left ventricle but also from the auriculo-ventricular angle, and attains a more vigorous growth than in the reptilian heart. The mouth of the aorta comes to occupy a position to the left of the interventricular septum in the mammalian heart (see fig. 24).

Pars membranacea septi.—There are really two membranous parts in the septum of the heart—without taking into account the septum ovale. One is interauricular; the other interventricular. The interauricular is situated in the auricular wall behind the central fibro-cartilage, and just above the base of the septal cusp of the tricuspid valve; it marks the point at which the endocardial cushions fused with the septum ovale. The other part is well known, and marks the fusion of the interventricular septum with the ventral endocardial cushion. It is separated from the interauricular membranous part by only the base of the endocardial cushion. The

aortic septal cushions do not reach down to the interventricular membranous area; all the muscular part of the septum is derived from the interventricular septum; I am not aware of muscular fibres ever appearing in the aortic endocardial cushions.

The auricular appendices.—Each auricle has primarily two poles, a cephalic and a caudal. In the cephalic pole of each ends the tænia sagitallis. It represents cephalic prolongation of annular band of the auricle (see figs. 17, 19 and 20). The tænia sagittalis can always be seen in the appendix of the right auricle in man (fig. 4). It represents the septum spurium (His). In the right auricle the cephalic pole remains as the appendix, the caudal disappears; in the left auricle, it is the reverse; the caudal pole persists; the upper, with its tænia sagittalis, disappear.

Finally.—If anyone will verify my conclusions, I would beg him, in repeating my experiments, to observe three necessary rules:

1. *That the basal attachments of the heart remain natural in position and uncut.*

2. That the chambers of the auricles are emptied of blood, by passing a stream of water through these chambers—at blood-heat, before any artificial or cast-taking material is injected.

3. If the 'heat-mass' (paraffin wax) injected is more than the ventricles can hold, then an opening must be made in the ventricle in order that the auricle may discharge its load and assume a state of complete contraction.

(4) Dr Peter Thompson showed *a heart* in which the inter-auricular septum presented two openings, one at the seat of the fœtal foramen ovale, and the other, one inch in front of the anterior limb of the annulus ovalis. The specimen, which was obtained from a male subject aged fifty-six years, is of special interest, not only because of its rarity, but also on account of its importance in connection with the development of the interauricular septum.

The opening at the seat of the fœtal foramen ovale resembled the most common form of patency to be observed in this situation, in that it was an oblique slit under the annulus on the right side and under a fold of endocardium on the left. The obliquity of the opening was such as to prevent the passage of blood from one auricle to the other. It was situated in the upper and left quadrant of the fossa ovalis, and admitted a probe a quarter of an inch in diameter. The floor of the fossa ovalis in its lower part was irregular, and crossed by thickened bands of endocardium. A specially developed endocardial band, under which a probe could be passed, stretched from the posterior limb of the annulus ovalis almost horizontally forwards, to be attached to the anterior limb.

The second opening was large enough to admit the tip of the little finger. Situated in front, and somewhat above the level of the fossa ovalis, and directly above the opening of the coronary sinus, it had important relationships to the bases of the ventricles. The septal cusp of the tricuspid orifice was immediately in front; the pars

membranacea septi was above and in front; a small intermediate cusp, uniting the inner extremities of the aortic and marginal segments of the mitral valve, projected into it on the left side. A feebly developed valvular fold of endocardium passed across the lower part of the orifice on the left side from the marginal cusp of the mitral valve.
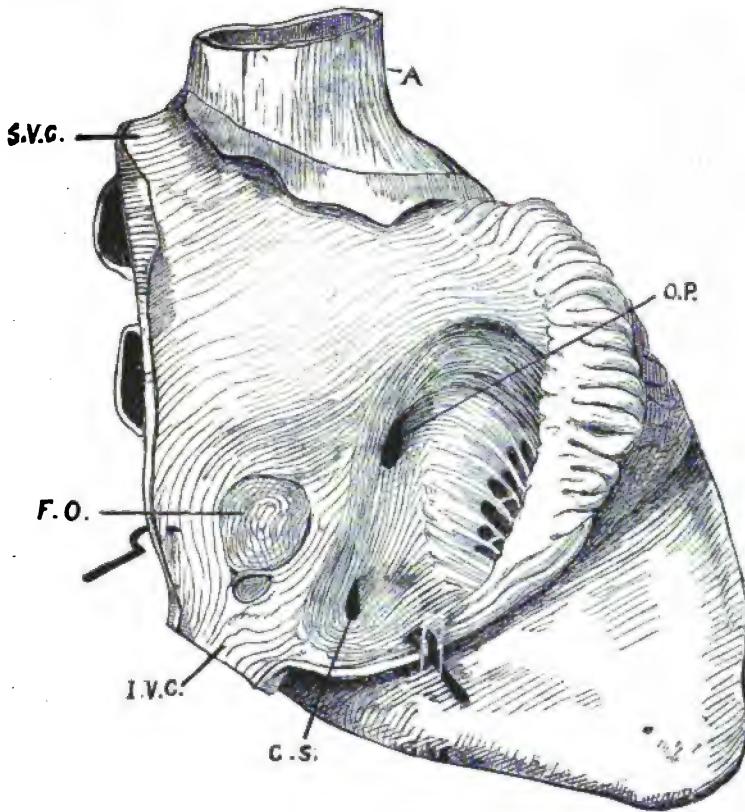
Heart showing persistent *ostium primum* in the interauricular septum. The right auricle has been opened in the usual manner and drawn from the right side. A, aorta; S.V.C., superior vena cava; F.O., fossa ovalis; I.V.C., inferior vena cava; C.S., coronary sinus; O.P., ostium primum.

The great interest of the specimen is centred in this rare opening in the interauricular septum. Obviously independent of the foramen ovale, an explanation of its occurrence must be sought by a reference to the development of the septum. The *septum primum* ought, in a normal course of development, to meet and fuse with the endocardial cushions. But whilst the process of growth towards the cushions is taking place, an orifice—the *ostium primum*—intervenes between the

cushions and the anterior concave edge of the primary septum. This is subsequently obliterated, but in the specimen now described it has persisted as a comparatively large opening, by means of which the two auricles are in free communication.

Whilst this seems to be the explanation of the abnormality, it is to be remembered that the pars membranacea septi is described as lying 'between the aortic vestibule on the left and the upper part of the right ventricle, as well as the lower and left part of the right auricle on the right."[1] The specimen seems to indicate that the closure of the ostium primum may be brought about by fusion of the upper and lower extremities of the septum primum with the endocardial cushions, and of its intermediate portion with the pars membranacea septi, and the ostium primum which has here persisted occurs between the anterior concave edge of the primary septum and the pars membranacea septi above and in front.

Arrests or abnormalities arising in the development of the inter-auricular septum seem somewhat rare.   Dr Keith showed to the Society in June 1898 a specimen in which the septum primum had fused with the left extremity of the auricular cavity, leading to the formation of a large right auricle and a small left auricle.   In this case the endocardial cushions, the aortic septum and the septum inferius were all absent.

Dr Peter Thompson also showed a specimen and lantern slides illustrating *an unusual form of mesentery enclosing small intestine, cæcum, and ascending colon.*

The specimen was found in a female subject aged 56 years, who died in the Middlesex Hospital.   For two months before death the patient had shown symptoms of intestinal obstruction, which commenced a few weeks after a fall from an omnibus.

At the post-mortem it was found that the small intestine, cæcum, and ascending colon were enormously distended, and that beyond the hepatic flexure, at which point the great omentum was bound down to it, producing a marked constriction, the great intestine was collapsed.   Moreover, there was a volvulus of the small intestine, cæcum, and ascending colon, and it was noticed that these three parts were enclosed in a common mesentery, which, however, did not extend downwards at its attached end beyond the level of the third lumbar vertebra.   This condition of the mesentery may perhaps be best explained by a reference to its development.

At an early stage of fœtal life, when the rotation of the intestinal loop has taken place, that part of the primitive mesentery contained within the concavity of the loop becomes the mesentery proper in the adult.   For a time it is continuous with the primitive mesentery of the large intestine, but subsequently the back of the mesenteries of the ascending and descending parts of the colon undergoes adhesion to the posterior abdominal wall and then disappears.   In the specimen now described, the mesenteric arrangement, so far as regards the ascending colon at least, conformed to the fœtal type; apparently

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[1] *Text-Book of Anatomy*, edited by D. J. Cunningham, F.R.S., p. 746.

there had been no adhesion to the posterior body-wall, and consequently no disappearance of its primitive mesentery.

It is interesting to note the influence of the embryological factor in the sequence of events. The injury would probably set up the local inflammation in the region of the hepatic flexure of the colon, resulting in the formation of peritoneal adhesions and narrowing of the gut. Then the ascending colon and cæcum, after becoming enlarged and distended, were thrown transversely across the abdomen, towards the left, in which position they were noted immediately on opening the cavity. The small intestine sharing in the general enlargement extended and filled up the right iliac fossa and right lumbar region, passing behind the cæcum and ascending colon. In this way the volvulus would probably be initiated, and when complete would result in a total intestinal obstruction.

(5) Dr R. J. GLADSTONE gave a preliminary communication on some cephalometric data bearing upon the relationship of mental ability to the size and shape of the head. His tables showed a distinct correlation between a high degree of mental ability and large size of head; that the increase in size of the head was due to an augmentation of all of its three principal diameters, namely, the longitudinal, transverse and vertical; and that in the adults measured, the increase occurred chiefly in the height of the head. The tables showed, further, that the increase in size of the head with an increase in the standard of mental ability was not only absolute, but also relative to the body-weight, the proportion of the (calculated) brain-weight to the body-weight being greater in individuals with a high standard of mental ability than in those in whom the standard was low. The figure indicating this relationship of the brain-weight to the body-weight Dr Gladstone termed the 'encephalosomatic index.' The paper, with the tables, will be published subsequently in the *Journal of Anatomy and Physiology*.

(6) Professor ALEXANDER MACALISTER demonstrated (1) an Egyptian *temporal bone* showing absence of the internal auditory meatus; (2) *a temporal bone* presenting a canal for the passage of the ninth cranial nerve; (3) a specimen in which the nerve to the crico-thyroid muscle passed through the thyroid cartilage.
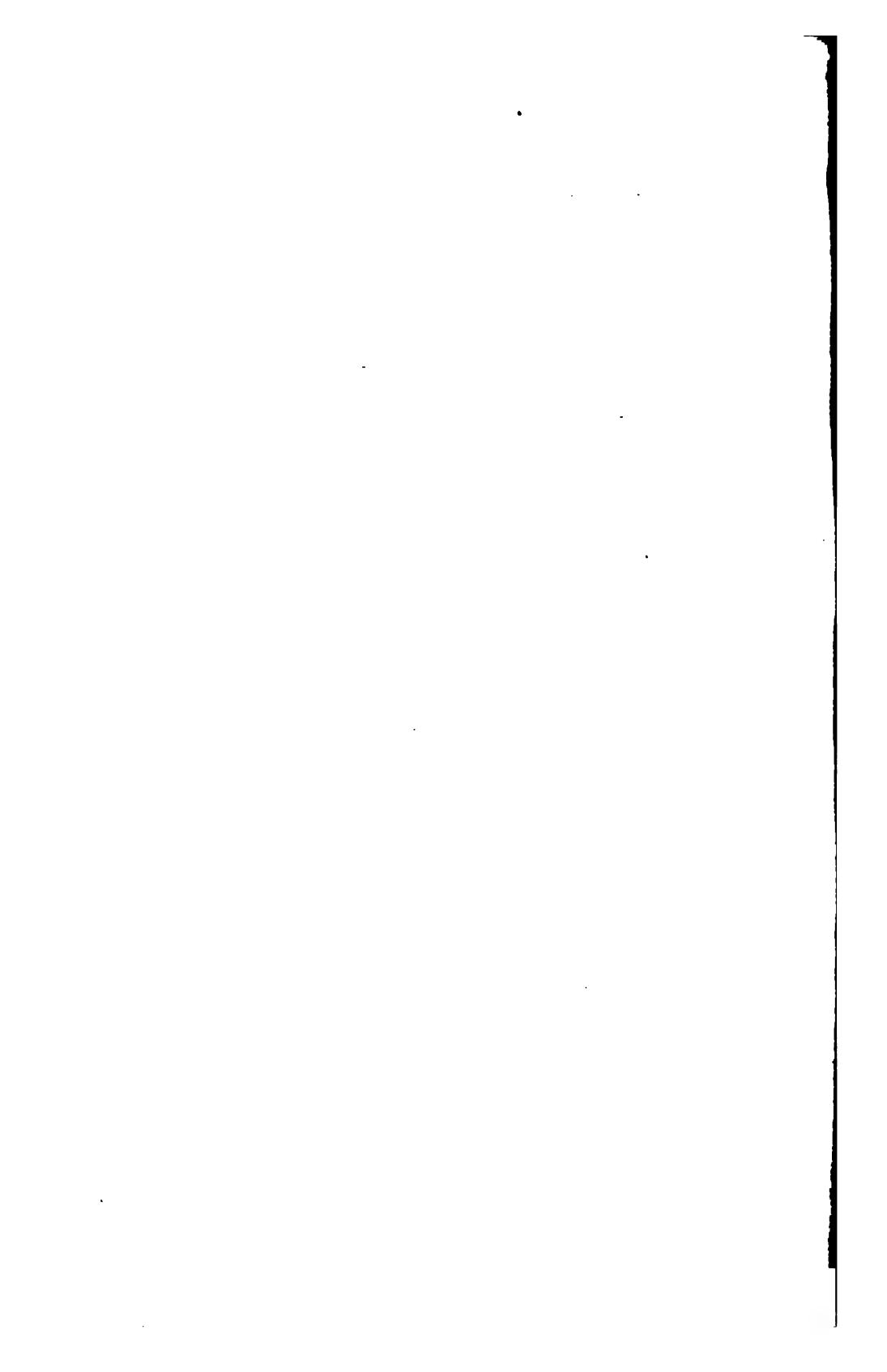
PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND.

JANUARY 1903.

An Ordinary Meeting of the Society was held at the Westminster Hospital Medical School, S.W., on Friday, January 30th, at 4 P.M. Mr C. B. Lockwood, the President, was in the chair, and thirteen members and two visitors were present.

The minutes of the last meeting were read and confirmed.

The following gentleman was unanimously elected a member of the Society :—Richard A. Stoney, M.B., Senior Demonstrator of Anatomy, Trinity College, Dublin, proposed by D. J. Cunningham, A. Birmingham, and Peter Thompson.

Specimens and Papers :—

(1) Mr F. G. Parsons read a paper *On the Meaning of Some of the Pelvic Centres of Ossification.* This paper will be published *in extenso* in the June number of the *Journal of Anatomy and Physiology.*

(2) Mr F. G. Parsons also gave a short communication *On the Obturator Tertius Muscle of Ungulates.* He pointed out that this muscle was originally described by Drs Mivart and Murie in the Hyrax, and has since then been noticed in several other ungulates.

It rises from the internal (pelvic) margins of the obturator foramen, and passes through that foramen to be inserted into the digital fossa of the femur. From a series of dissections of ungulates carried out in conjunction with Professor Windle, he was convinced that this is not a separate muscle, but part of the obturator externus, which has pushed its way inward through the obturator foramen, and has stolen

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the normal attachment of the obturator internus. His reasons for this conviction are (1) that it is inseparable from the obturator externus outside the pelvis; (2) that the delicate obturator membrane is to be made out pushed inward in front of it; and (3) that the obturator nerve supplies it. It appears that the muscle is present in this form in the Artiodactyla and Hyrax (Procavia), but not in the Perissodactyla. He did not at present know whether it is to be found in the Cervidæ or Elephantidæ.

(3) *Homologies of the Sense Organs.*   By JOHN CAMERON, M.B., M.R.C.S.   (*Abstract.*)

The question of the homologies of the various sense organs has been keenly discussed, and there is still much doubt regarding the comparison of the different parts of the sense organs with one another. In *Quain's Anatomy* (vol. iii., pt. iii., p. 152) it is stated that the ganglion cells on the posterior roots represent the sense epithelium, such as we find in the olfactory organ and in the retina of the eye. The result of this would be to ignore the stratified epithelium of the skin altogether, and consider it as having nothing to do with the reception of tactile impressions. A little further on in the same page of this work, the cells of the spinal ganglia are compared to the specialised cells which are found lying between the epidermal cells of lumbricus, and whose short distal processes end on the free surface, while their long central processes arborise around ganglion cells. The mode of development of the spinal ganglion cells is sufficient to oppose this theory, for they always remain close to the developing nerve centre, and their distal processes grow towards the periphery, and, moreover, never reach to the free surface, but ramify amongst the cells of the stratum Malpighi. The cells of lumbricus resemble more highly specialised epithelium cells, such as the vertebrate olfactory cells, and the latter are the only sense epithelium cells of vertebrates, which develop in such a manner that their distal processes remain on the free surface, while their proximal processes grow towards the nerve centre. The writer would thus look upon the cells of the stratum Malpighi as the tactile sense epithelium, and this view is supported by the fact that the epithelium of the touch corpuscles is developed from the epidermis.

Four stages may be noted in the reception and transmission of tactile impulses. There is, firstly, the sense epithelium, which is represented by the stratum Malpighi. The second stage is formed by the spinal ganglion cell, with its distal and central processes. There is, thirdly, the stage of relays within the nerve centre (nucleus gracilis or cuneatus and optic thalamus). The cerebral cortical cells constitute the fourth and last stage.

The sense epithelium for hearing consists of the auditory cells, which are developmentally homologous with the cells of the epidermis. The cell of stage ii. is situated in the spiral ganglion, and, like the spinal ganglion cell, it is formed from the neural crest. The

stage of relays consists of the accessory nucleus or tuberculum acusticum, and the median geniculate body, posterior corpus quadrigeminum or superior olive. Stage iv., the same as above.

The gustatory sense epithelium is found in the taste-buds. The writer considers the cell of stage ii. as being situated in the Gasserian ganglion, and, if this be so, it corresponds developmentally with the cell of stage ii. in the tactile and auditory senses. Stage iii. consists here of one relay in the vicinity of the fourth ventricle and one in the optic thalamus (both are hypothetical). Stage iv., the same as above.

The olfactory cells are, as regards their development, homologous with the auditory and epidermic cells. Stage ii. is represented by the mitral cells of the olfactory bulb. With regard to stage iii., Elliot Smith finds that in monotremes there is only one relay (fimbria, fascia dentata, septum lucidum or peduncle of corpus callosum). Stage iv., the same as above. There has always been a difficulty in comparing the retina with the other sense organs, on account of the numerous layers in the former. The writer has found, however, that in the chick and tadpole, some of the bipolar cells of the inner nuclear layer migrate through the external molecular layer, and become transformed into rod and cone cells, and on this account the inner and outer nuclear layers of the retina together correspond to the epithelium of the other sense organs. Stage ii. is formed by the retinal ganglion cells. There is only one stage of relays (lateral geniculate body, pulvinar or superior corpus quadrigeminum). Stage iv., the same as above.

On reviewing the subject generally, it will be observed that the arrangement throughout the different stages in the tactile, auditory and gustatory senses is very similar. The sense epithelium cell has no central process, the cell of stage ii. is practically the same in all, and stage iii. consists of two relays within the nerve centre. The arrangement for the olfactory and visual senses also agrees very closely. The sense epithelium cell possesses a central process, the cell of stage ii. is somewhat similar (multipolar) in both cases, while in stage iii. there is only one relay within the nerve centre.

(4) Mr N. BISHOP HARMAN showed a brain and lantern slides exhibiting the effects presumed to be produced by a *bullet wound of the brain* in a man, as determined by its experimental production in the cadaver.

A soldier was shot in South Africa whilst asleep. The bullet (a small gauge hard-cased missile) entered by the parietal bone $2\frac{1}{2}$ in. from the ext. angular process, and $4\frac{7}{8}$ in. up from Reid's base line, and escaped through the occipital bone 1 in. up from the ext. occipital protuberance, and $\frac{1}{2}$ in. to the left of the median line. The man was unconscious for a fortnight; recovered with right paraplegia and right homonymous hemianopsia, the paresis diminished until there remains only some weakness of the right arm, the field of vision had not changed, but central vision was full.

The head of a cadaver, the proportions of which were ascertained by the usual anthropometry to coincide with those of the patient's, was injected with formaline shortly after death. The wound sites were found, trephined, and from hole to hole a stylette passed, and over it a tube of the size of the bullet pushed.

Examination of the skull showed that neither meningeal vessels of any size nor any venous sinuses were damaged. The probe entered the brain in the ascending parietal convolution just below the level of the sup. frontal sulcus, and, passing under the supra-marginal convolution, angular gyrus, and middle occipital convolution, escaped at the posterior inferior junction of the last with the cuneus. Sections showed that the wound had dominated the grey areas of these regions in a remarkable manner, besides penetrating the greater part of the occipito-thalamic radiation. The position of the entrance wound and the transience of the motor paresis was thought to lend support to the new localisation of the motor area in anthropoids by Sherrington and Grünbaum. The hemianopsia was fully accounted for by the destruction of the occipito-thalamic radiation. A feature of the fields of vision was a rim of blindness on the left side of the left eye; it was thought this might suggest some lesion of the right hindpart of the cuneus near the middle occipital convolution, by reason of the nearness of the site of the wound of exit to this area.

(5) *On a Case of Congenital Cardiac Malformation.* By Dr F. H. THIELE. (This specimen was exhibited before the Society in November 1901.)

Clinical History.—The patient from whom this heart was obtained was a boy three and a half years old. He was admitted to University College Hospital under the care of Dr S. Martin, suffering from broncho-pneumonia with a great deal of cyanosis.

The mother stated that prior to his illness he never was 'blue,' but that he was unable to run about like her other children.

A loud systolic murmur was heard, having its maximum intensity at the pulmonary cartilage. The murmur was heard over the whole cardiac area.

Description of the Heart.—The heart is divided into two auricles and two ventricles, the auricles communicating with one another by a wide orifice, and the ventricles by a minute opening at the un-defended spot.

The right auricle receives the superior and inferior venæ cavæ together with the coronary sinus. The right ventricle gives off the aorta from which the coronary arteries arise. The branches from the aortic arch are normal in number and relation, and there is no communication between the aorta and the pulmonary artery. The left auricle receives the four pulmonary veins, and the left ventricle gives off the pulmonary artery.

The Cavities of the Heart in detail.—The right auricle is a large cavity, having a diameter of just over 2·5 cm. The auricular appendix is a large muscular process, and has the normal relations.

The opening from the auricle into the appendix is 2 cm. wide, and the appendix is 2·5 cm. long. The average thickness of the wall of the appendix is 2·5 mm. Entering the auricle just above and behind the auricular appendix is the superior vena cava, below is the inferior vena cava. There is a well-marked delicate Eustachian valve from which a slender filament runs to the Thebesian valve, uniting the free edges of the two valves. The opening of the coronary sinus is in its normal position. The inter-auricular septum is incomplete at the upper part, the deficiency in the septum being one centimetre in diameter. This deficiency is divided by a thin vertical band into a posterior smaller and an anterior larger area. Below the opening the floor of the fossa ovalis is formed by a firm cribriform membrane, which membrane is funnel-shaped, the closed apex of the funnel at the autopsy projecting into the right auricle.

The right ventricle has a cavity 7 cm. in length and 2·5 cm in transverse diameter. The average thickness of the wall is 1·5 cm., and the heart's apex is formed by the right ventricle. The auriculo-ventricular valve is tricuspid ; the musculi papillares have the normal arrangement. The valve and the chordæ tendineæ are thicker on this side than on the left side of the heart, but the reverse is the case with the musculi papillares. At the highest part of the cavity is the aortic orifice, separated from the auriculo-ventricular orifice by an infundibulum 30 mm. long. The upper wall of the infundibulum is formed by the muscular prominence which is named by His the supraventricular crest, and which, in the normal heart, contains the beginning of the aorta, but in this case lodges the pulmonary artery. The aorta arises in front of and rather to the left of the pulmonary artery, passes upwards and backwards above that trunk to form the arch in the usual position above the root of the left lung. The vessels arising from the arch are normal in arrangement. The two coronary arteries arise from this trunk from the Sinuses of Valsalva over the posterior and left anterior aortic flaps. There is a normal aortic valve with three semilunar flaps, which appear to be right and left anterior and one posterior. The minute interventricular opening is placed under cover of the anterior corner of the septal flap of the tricuspid valve.

The left auricle is much smaller than the right, and its wall is about 1·5 mm. in thickness. Its appendix is long, narrow, and tortuous. The four pulmonary veins open into the auricle in the normal way.

The left ventricle is smaller than the right, its cavity being 5 cm. long and 2 cm. wide, and the wall is 6 mm. thick. It gives off the pulmonary artery, which arises behind and rather to the right of the aorta. Its divisions are normal, and there is no sign of the ductus arteriosus being patent. The pulmonary valve is normal, with three semilunar flaps, which appear to be an anterior and right and left posterior. The pulmonary trunk is directed backwards and to the right behind the origin of the aorta and the infundibulum of the right ventricle ; and somewhat to the right of and below the aortic

arch it divides into the usual two branches. The lungs are normal, the right lung having three lobes and the left two. The left auriculo-ventricular valve is bicuspid, but is not so strong as usual, and not so strong as the valve of the right side, though the papillary muscles are stronger. On this side the interventricular opening is placed 3 mm. below the attached margin of the right posterior flap of the pulmonary valve and a little behind its centre. This opening is clearly in the undefended spot, and will only admit a fine bristle.

Similar cases are recorded in the second edition of Dr Peacock's *Malformations of the Human Heart.* He quotes from Virchow's *Archiv. of Path. Anat. and Phys.*, 1857, vol. xii. p. 364, a case of Friedberg's, in which the foramen ovale was open, the ductus Botalli and the septum of the ventricles closed. Another case was published by Dr Cockle in the *Medico-Chirurgical Transactions*, vol. xlvi. p. 193. "In a male child, which survived two years and eight months, and was cyanotic. Septum of ventricles entire, foramen ovale completely open, ductus arteriosus obliterated. The aorta arising from the right ventricle and the pulmonary artery from the left."

There are numerous other cases recorded of transposition of the aorta and pulmonary artery, but in these cases, with the exception of the two quoted above, either the septum between the ventricles was more or less incomplete, or the ductus arteriosus was patent. In other cases, not only have the arteries been transposed, but the ventricles also, as was indicated by their relative size and the form of the auriculo-ventricular valves.

The mode of origin of this abnormality may, I think, be explained by an abnormal rotation of the septum of the common arterial trunk. According to His, this septum is formed by two ridges projecting into the common tube. These ridges are so placed that at the upper end they are disposed sagitally, being anterior and posterior, so that the resulting tubes are side by side; at the lower end the ridges right and left, and the tubes, are anterior and posterior. The meeting of these ridges and the consequent formation of the tubes occurs from above downwards. Now, in the normal condition, if we imagine the upper end to be the starting position of the septum, it will be seen that the anterior margin of the septum above comes to be the right margin below, and thus the septum rotates through 90° in the direction of the hands of a watch. Accordingly, at the upper end, the two vessels lie side by side, the aorta being to the right, the pulmonary artery to the left, and tending to pass behind the aorta. At the lower end, the pulmonary artery lies in front of and a little to the left of the aorta.

The condition of things and the mode of rotation of the septum will be seen from the accompanying diagrams, which represent sections of the arterial trunks at different levels. (Diag. A.)

In the specimen here described there exists at the upper end the same arrangement of vessels as in the normal, whilst at the lower end the aorta arises in front of and a little to the left of the pulmonary artery. This may be explained by rotation of the septum in the

opposite direction, viz., 90° contrawise to the hands of a watch, and thus the anterior margin of the septum above is turned to the left below, instead of to the right, as in the normal.
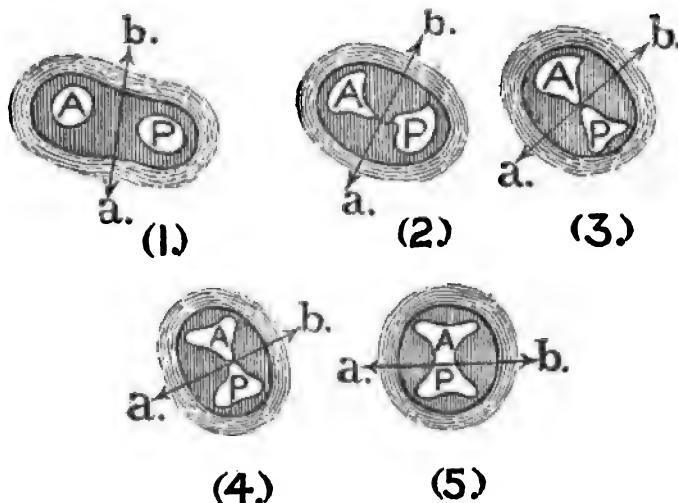

DIAGRAM A.

Fig. 1 being the highest, and fig. 5 the section just above the heart.   A. represents the aorta ; P. the pulmonary artery ; (a, b) the septum—(a) being the anterior, (b) the posterior margin.
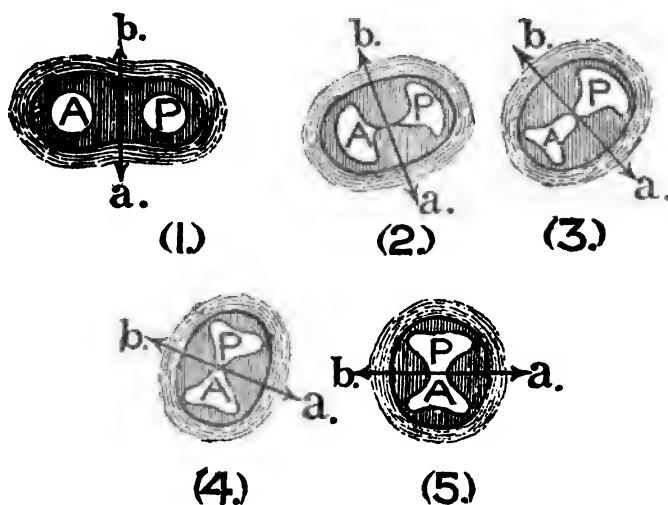

DIAGRAM B.

A similar series of diagrams to the above, with the same lettering and arrangement, indicates this (diag. B), and by this means the aorta comes to lie in front of the pulmonary artery.

The rotation of the septum in the two cases is shown in the following diag. C.
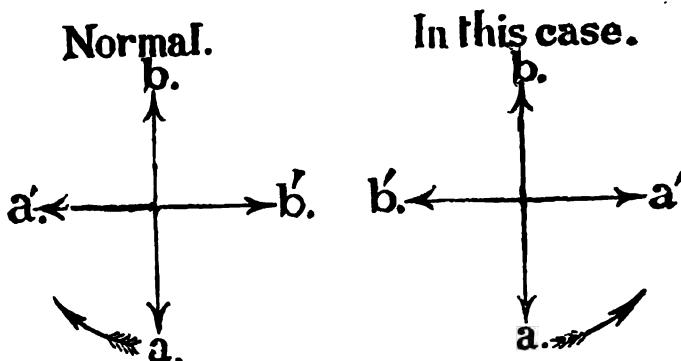

DIAGRAM C.

This abnormality also finds a place in Rokitansky's scheme. According to him, the common arterial trunk is divided into the two great trunks by an asciform septum, which is so placed that its convexity lies forwards and to the left. Thus in (1) diag. D, *ss'* is the septum, (P) the pulmonary artery, and (A) the aorta. Now, by alterations in the position of the septum, the relative positions of the vessels may alter; thus, if *ss'* of (1) be conceived rotated through 180°, the position of the vessels occurring in this specimen is obtained, as is represented in (2) diag. D, the aorta lying in front of and to the left of the pulmonary artery. This will account for the transposition of the vessels. According to Rokitansky two conditions may exist with transposed vessels :—

1. The transposed vessels may open from physiologically incorrect ventricles.

2. The vessels may open from physiologically correct ventricles.

Case 1 he calls uncorrected transposition.

Case 2 he calls corrected transposition.

These results, according to Rokitansky, are due to variations in the position of the attachment of the ventricular septum to the vessels. This septum he supposes to grow upwards towards the arterial septum, and in its direction. It is normally inserted into the anterior and left part of the aorta, whence it encircles the right side of the vessel; the pars membranacea continues this attachment along the border of the posterior flaps, and is inserted into the diametrically opposite point in the aorta. In any anomalous position of the two vessels the pars membranacea always lies along the convex border of the posterior

vessel, either along its right or left side, no matter whether it be the aorta or pulmonary artery.

Thus if it pass to the right of the posterior vessel, that vessel will be relegated to the left ventricle ; if to its left, then the vessel will arise from the right ventricle.   The septum rarely passes to the same side of both vessels.

Thus in diag. E, modified from Rokitansky's figures, in (1) we have the normal condition of things, the septum being inserted into the anterior and left part of the aorta and the pars membranacea along the right border of the aorta.   In (2) we have transposition of the vessels with normal arrangement of the septum, and so we get 'uncorrected' transposition, and this is what has occurred in the specimen now described.

In (3) diag. E the pars membranacea passes along the left of the posterior vessel, and this is Rokitansky's 'corrected' transposition of the vessels, of which there are several cases recorded.


DIAGRAM D.

POSTERIOR.   POSTERIOR.

(I.)   ANTERIOR.   (2.) ANTERIOR.

POSTERIOR.

(3.) ANTERIOR.
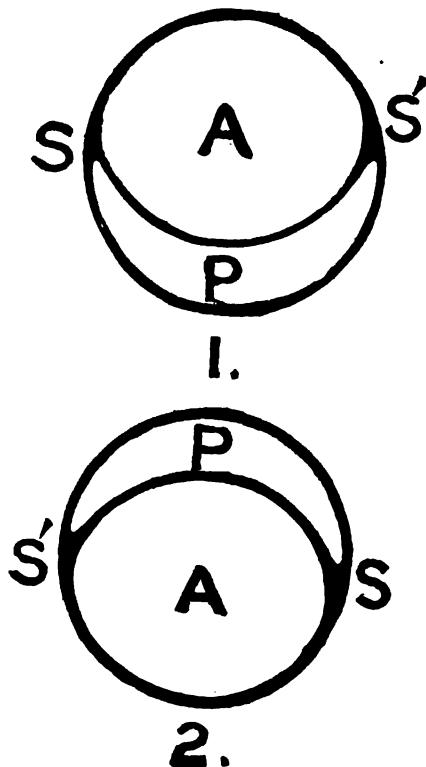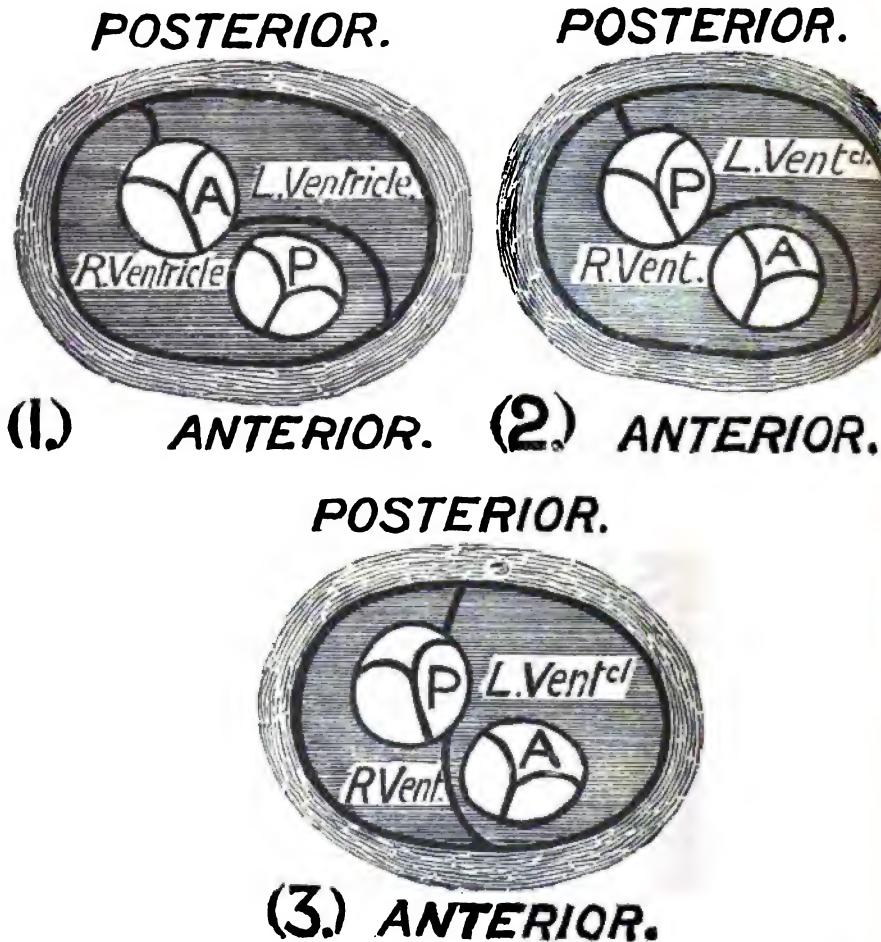
DIAGRAM E.

Diag. A is copied from His' *Menschliche Embryonen.* D and E are after Rokitansky.

I have to tender my best thanks to Prof. S. Martin for permission to publish the case, and to Prof. G. D. Thane for his valuable advice as regards the specimen.

PROCEEDINGS OF THE

ANATOMICAL SOCIETY OF GREAT BRITAIN

AND IRELAND.

MAY 1903.

An Ordinary Meeting of the Anatomical Society of Great Britain and Ireland was held at the London Hospital, Whitechapel, E., on Friday, May 1st, at 4 p.m.   Mr C. B. Lockwood, the President, was in the chair, and seventeen members and four visitors were present.

The minutes of the last meeting were read and confirmed.

Specimens and Papers :—

(1) *Contributions to the Human Mechanism of Respiration.*
        By Arthur Keith, M.D.

The manner in which the apices of the lungs are expanded and filled with air is a matter of the utmost clinical importance.   While it is probably true that their susceptibility to tuberculosis is due to an imperfect expansion or inflation with respiratory air, yet no satisfactory explanation has been offered of their imperfect expansion or inflation.   Wherein lies the defect in the inspiratory mechanism? The following observations deal first with certain neglected points in the structure of the upper part of the thorax which have to do with the expansion of the apices of the lungs.

The sterno-manubrial joint.—The movements at this joint may be studied in the following three ways : (1) In the living by applying two small reflecting mirrors ($\frac{1}{2}$ inch diameter), one over the manu-brium, one over the mesosternum, and throwing their reflections on a screen at a fixed distance from the person examined.   The easiest manner of fixing the mirrors to the sternum is by mounting them on small rubber bell-like ' suckers,' such as are used for fixing objects to the glass of shop windows.   Mirrors mounted in this manner serve to demonstrate the movements of the heart if placed over the area of cardiac impact.   (2) The movements of the joint may be measured

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in life by using a minute pendulum. By means of two rubber suckers, such as are mentioned above, two levers are attached, one at right angles to the manubrium, the other to the mesosternum; from the point of each lever a minute pendulum is suspended, the ball of which swings in front of a scale graduated in degrees. These may be applied either in the lying or standing posture. (3) The movement may be studied and measured after death by performing artificial respiratory movements in the right or left half of a thorax from which all the parts, save the ligaments, have been removed. By applying the cut or mesial surface of such a thorax to a wide board, and fixing the spinal column to the applied surface by nails, tracings of the sternum in various stages of a complete respiratory movement may be obtained.

The extent of movement at the sterno-manubrial joint.—The extent varies with the individual, with the sex, with disease, with the type of respiration, and with the degree of the respiratory act; but the essential fact concerning it is that there is no elevation or headward movement of the *primate* sternum possible without a movement at this joint. In a collie dog, which submitted voluntarily to an examination, there was no movement at this joint, but in it there was no forward or headward movement of the sternum; in this particular dog the movement of the sternum was one of pure rotation, the abdominal end rotating downwards and forwards in placid respiration 4° to 6°.

The following were the movements at the sterno-manubrial joint as measured by the rotation of the anterior surface in five individuals —two men, one woman, two children—all in a state of health:—

	Manubrium.		Mesosternum.	
	Moderate Inspiration.	Full Inspiration.	Moderate Inspiration.	Full Inspiration.
Man A,	2–3° upward	13–14° upward	1–2° downward	3–4° downward
Man B,	1–2 ,,	6–7 ,,	no rotation	1° ,,
Woman,	3–4 ,,	12–14 ,,	2–3° upward	6–8 upward
Children (6–8 years)	2–3 ,,	4–5 ,,	1–2 ,,	3–4 ,,

Thus in complete inspiration the degree of movement at the sterno-manubrial joint was as much as 18° in man A; in the woman, although the actual rotation of the manubrium was as great as in man A, yet the movement at the sterno-manubrial joint was only 6°, owing to the mesosternum undergoing a rotation in a direction similar to that of the manubrium.

The function of the sterno-manubrial joint.—In estimating the part this joint plays in the inspiratory expansion of the lung, one has to consider the significance of (1) the width, the strength, the early liability to ossification of the first costal cartilage and its direct continuity with the manubrium; (2) the peculiar shape of the first rib; (3) the peculiar costo-vertebral articulation of the first rib; (4) the attachment of Sibson's fascia, the subclavian and innominate veins to the first rib. Taking all of these points into consideration

so that their functional meaning may be explained, and by observing the respiratory movement in the living, one must .conclude that the manubrium sterni, the first pair of ribs and their cartilages, with Sibson's fascia, form a functional lid for the thorax, and move as if they formed one piece. The lid is hinged to the vertebral column at the first costo-vertebral articulation ; its movable or swinging end is attached to the anterior wall of the thorax at the sterno-manubrial joint. The anatomical and physiological apex of the lung lies above the level of the upper border of the second costal arch.

The inspiratory expansion of the apex of the lung.—Since the vertebræ and the vertebral segments of the ribs (defining the vertebral segment of a rib as that part which is covered by the erector spinæ or its prolongations) encroach on, rather than enlarge, the cavity of the thorax during an inspiratory movement, there can be no expansion of the apex of the lung in a backward direction. In considering the expansion of the apex in a forward direction, one must remember (see fig. 1) (1) that it slopes downwards and forwards
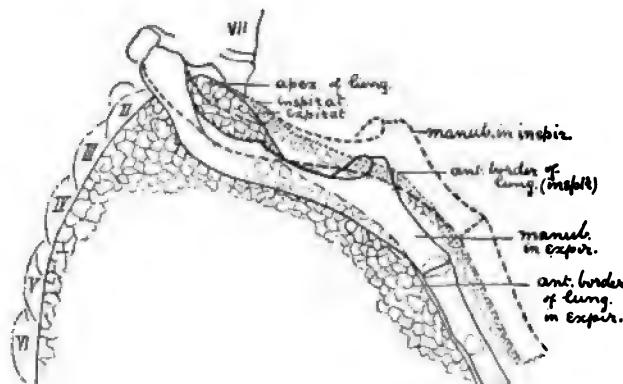

FIG. 1.—A figure to show the relationship of the first rib and manubrium sterni to the apex of the lung (1) in expiration, (2) in inspiration.

from the neck of the first rib to the upper border of the second costal cartilage ; (2) that on this sloping surface there are placed Sibson's fascia, the first rib, the subclavian artery, and the subclavian vein, all of which form the thoracic lid. The lid is hinged behind ; when its anterior part is lifted up on inspiration, it is the anterior part of the apex that feels the movement; the posterior part lying in front of the neck of the first rib, being nearer to the axis of movement, is only affected indirectly (see fig. 1). The lowest trunk of the brachial plexus crosses the first rib almost in the axis of the movement, and is but little disturbed. Thus the upward movement of the thoracic lid is not effective in causing an expansion of the dorsal part of the apex of the lung.

If, however, one turns to the lateral expansion of the thorax, a more effective and direct agent for bringing about the expansion of

the lung will be found. In fig. 2 is represented the characteristic 'bucket-handle' movement of the five upper ribs—a movement peculiar to the upper five ribs. In this movement the bow of the costal arc is elevated on an axis joining the spinal and sternal extremities. This movement brings about a direct lateral expansion of the apex of the lung, but it will be noted that the part of the
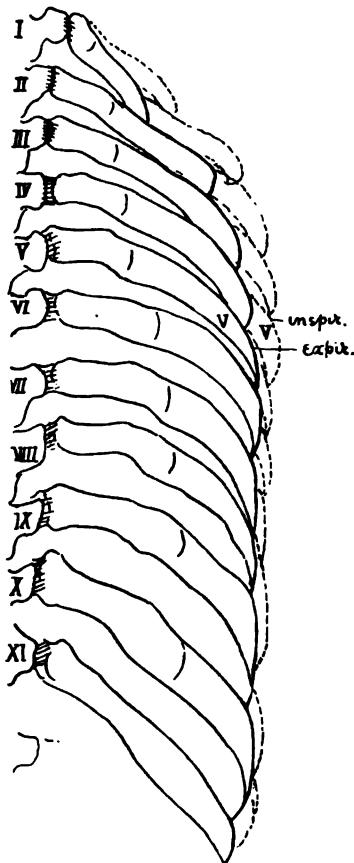

FIG. 2.—The right half of a thorax viewed from behind. The position and outward expansion of the lungs during inspiration are shown by dotted lines. The lateral expansion is seen to be obtained by the movements of the upper five ribs.

apex in front of the neck of the first rib is the least affected by this movement.

There is still one other direction in which the apex of the lung may expand, and that is towards the diaphragm or floor of the thorax. In the quiet abdominal type of respiration the diaphragm is certainly the

principal agent in causing an expansion of the apex.   A respiratory
contraction of the diaphragm causes a descent of the whole lung, the
basal part being first affected and moving most, the apical part being
last set in motion and moving least.

Thus it will be seen that of the three forces which may cause an
expansion of the apex of the lung, one of them only, the upward
rotation of the costal arcs, acts directly; while the other two, the
upward movement of the thoracic lid and the downward movement of
the diaphragm, act only indirectly.   Further, that it is the dorsal part
of the apex of the lung, that part which lies in front of the neck of the
first rib and first intercostal space, that has the least effective provision
for its expansion of all the parts of the lung.

*Certain unexplained points in the structure of the lower six
costal arcs.*—In teaching the structural mechanism of respiration,
one feels the necessity, in order to make the matter simple and easily
understood, of treating the costal movements, which lead to an
enlargement of the thorax, as if they were the same in each rib.
Yet all of those who have paid special attention to this subject have
noticed that each rib has its own peculiar combination of movements,
has its peculiar articulations and its peculiar shape; but, as a rule, these
individual features are dismissed as of no real import in practical
medicine.   There is, however, one series of adaptational structural
points which characterise the second, third, fourth, and fifth pairs of
ribs, and another series which are found in the seventh, eighth, ninth,
and tenth pairs, while the sixth pair is always intermediate in structure
to the upper and lower costal sets (see fig. 3).   I am unable to offer
a full and adequate explanation of the differences of structure between
these two sets of ribs, but I wish to place them on record here, because
their significance will certainly become apparent to whoever succeeds
in mastering the true movements of the ribs.   The same distinction
in structure between the upper and lower sets of ribs is to be seen in
the thorax of all orthograde primates.

In the upper set of ribs (second, third, fourth, fifth), when
the thorax is viewed in profile, each rib is seen to be bent,
with its lower margin showing a convexity from the angle to the
costo-chondral junction (fig. 3); the convexities are directed down-
wards to the sixth rib.   In the lower set (seventh, eighth, ninth, tenth)
the upper border is convex, the convexity being directed upwards to
the sixth rib (fig. 3).

One explanation of this is to be found in fig. 2.   The upper set of
ribs is seen to be raised by a 'bucket-handle' movement, and thus
expanding the chest laterally.   The lower set undergo no such move-
ment; they are long levers articulated at their vertebral ends; when
their ventral ends are raised, they lead to a great lateral enlargement
of the abdominal wall, but only to a very partial lateral enlargement
of the real pulmonary space.   That is to say, while the upper set of
ribs are direct lateral distenders of the lung, the lower set is made
accessory to the diaphragm.   They provide a fulcrum for the diaphragm;
their lateral movement is designed to make room for the abdominal

viscera displaced by the diaphragm rather than to cause a direct
enlargement of the lung.

The upper and lower costo-transverse articulations.—As is well
known, the costo-transverse articulations of the upper and lower sets
of ribs show a marked difference in form, but the meaning of this
difference is not easy of explanation. In the upper set the articular
facet on the rib is oval and convex, as if it were the segment of a
cylinder; while the facet on the transverse process is socket-shaped,
so as to receive the costal articulation (fig. 4). In the lower set of ribs
the costal and transverse facets are flat and oval (fig. 4). The costo-
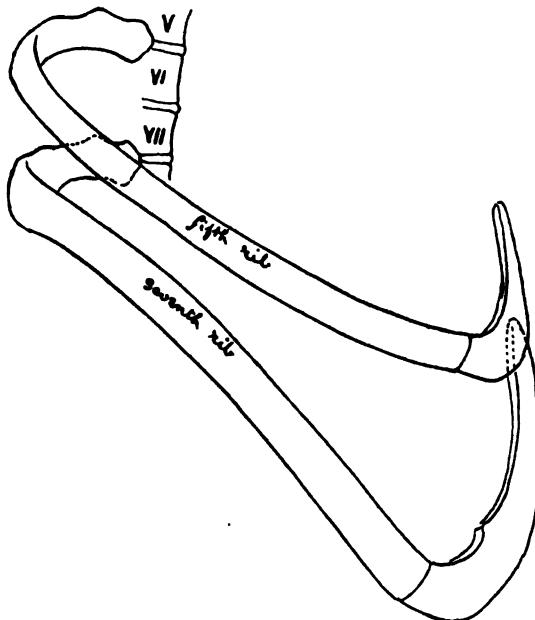

FIG. 3.—A drawing of the fifth and seventh ribs of the right side *in situ*, to show
the differences in shape which distinguish the upper and lower sets of ribs.

transverse articulations of the sixth rib are intermediate in character.
What is the explanation of this difference? In the first place, the lower
set is acted on by the diaphragm, while the upper set is not; the upper
set undergoes an upward rotation round a sterno-vertebral axis, while
the lower does not.

The axis round which the ribs rotate.—The most accurate repre-
sentations of the respiratory movements of the ribs are those given by
Thane in *Quain's Anatomy*, vol. ii. part ii. p. 161 (ed. 10). The
axis of rotation there shown passes through the neck of the rib; for
all practical purposes such an axis may be accepted as correct. But
it is not absolutely correct. On comparing horizontal tracings of the
thorax, taken by narrow plates of lead during life, I was struck by

the forward movement of the vertebral segments of the lower ribs (fig. 5). In over half of the subjects I investigated—nine in all—the thorax underwent a diminution on its dorsal wall instead of an enlargement during inspiration. On examining the movements of the ribs on an artificially prepared thorax, in which the life-movements were imitated, that part of the rib on which the tubercle is situated was found not to be part of a stationary axis, but underwent during inspiration a movement forwards and downwards, so that, at the end of an inspiratory movement, the tubercle, and segment of the rib on which the tubercle is situated, occupy a lower and more ventral position in relationship to the transverse process than at the commencement of the inspiratory act. Further, most writers on this
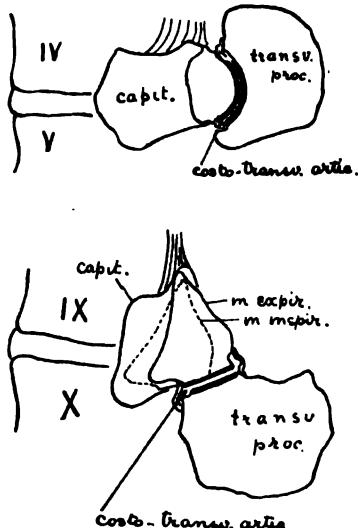

FIG. 4.—The costo-transverse articulations, as seen in section, of the fourth and ninth ribs.

subject overlook the fact that the ilio-costalis is attached to the ribs, and actively or passively must be concerned in the respiratory movements of the ribs. The ilio-costalis is attached only to the lower set of ribs—those with the flat oval costo-transverse articulations to which the diaphragm is also attached, and which undergo a slight downward and forward movement at their vertebral segments.

The ilio-costalis as a respiratory muscle.—So far as I know, no one has ever offered any explanation of the peculiar arrangement of the outer column of the erector spinæ, or attached any meaning to its relationship to the ribs. On attempting to imitate in a large model the respiratory movements of the seventh rib, I found that unless a stay were attached to the rib at its angle, so as to represent the ilio-costalis, the movement obtained from the external intercostal sheet

of musculature was one similar to the upper ribs—namely, a 'bucket-handle' movement—attempting thus to give a lateral expansion of the chest. But, on applying to the rib a cord attached at its angle so as to represent the ilio-costalis, I could produce in the model an exact copy of the normal movement of the lower ribs. The further evidence, perhaps not of great weight, may also be stated: that a hand placed over the ilio-costalis during full or moderately full inspiration feels that muscle to harden as if then in increased action. Further, in people who have suffered from rheumatoid arthritis of the costo-vertebral articulations, the pathological heapings of bone at the
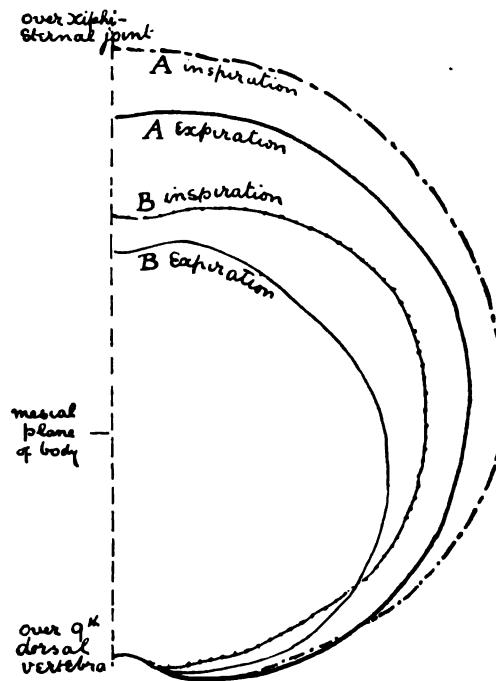

Fɪɢ. 5.—Horizontal tracings of the right half of the body of two individuals in expiration and inspiration. The tracings were taken at the level of the ninth dorsal vertebra and xiphi-sternal joint. The two individuals represented in the figure show a marked difference in the degree of flattening in the posterior wall of the thorax during inspiration.

margins of the costo-transverse articulations could only be accumulated if a forward and downward movement occurred at the costo-transverse articulation during inspiration. The upward convexity of the lower set of ribs, as seen in a profile of the thorax (see fig. 2), is evidently the result of the insertion of the ilio-costalis to this set; the ilio-costalis provides a movable fulcrum for this set of ribs. The ilio-

costalis is neither a muscle of inspiration or expiration; it is in action steadying the lower ribs during both acts, but its exertion is greatest during inspiration. The accessorius unites the lower or diaphragmatic set of ribs to the upper, on which it acts as a muscle of expiration. The cervicalis ascendens, as far as it is respiratory in function, is the inspiratory opponent of the expiratory accessorius.

The interchondral articular facets.—What is the meaning of the articulations which are found between the sixth, seventh, eighth, and ninth costal cartilages? Out of nineteen bodies I examined, thirteen had, besides the articulations between the sixth, seventh, eighth, and ninth, also one between the fifth and sixth. These facets are to be seen in the fifth-month foetus. In the great anthropoids the sixth, seventh, and eighth cartilages come together, and synovial facets are found, but the great heels of cartilage which are thrown out at these articulations are found only in the human thorax. There are neither facets nor heels, nor direct contact between the cartilages, in any of the pronograde primates.

The explanation of these interchondral facets offered by Hermann von Meyer in the *Archiv für Anatomie*, Anat. Abth., 1885, p. 277, is, I believe, the correct one—viz., that through these interchondral articulations the diaphragm may exert its lifting force on ribs above those to which it is attached.

The three segments of a costal arc.—A prolonged examination of the respiratory mechanism of reptiles, birds, and mammals has convinced me that in all forms each complete costal arc constantly shows three segments, each of which has its physiological significance. Each of these segments bears a definite relationship to the corresponding segment in the costal arc in front of it and behind it. The three segments are dorsal, lateral, and ventral. The *dorsal* is that covered by the erector spinæ; the *ventral* is represented by the costal cartilages, the *lateral* by the intermediate section of the arc, between the dorsal and ventral. The ventral segments invariably increase in length and obliquity in passing from the cervical to the abdominal border of the thorax. The same law holds good for the dorsal segment, except that in primates the dorsal segments of the middle ribs are the least sloping; in approaching the cervical border, as in passing towards the lumbar border, the inclination towards the spine becomes increasingly marked. As regards the inclination of the *lateral costal segments*, they also become more oblique in position as one passes from the cervical to the abdominal border of the thorax. In primates the lateral costal segment increases in length up to the sixth, or occasionally to the seventh rib; beyond that it rapidly declines, this segment being only partially represented in the eleventh rib. Thus each half of the thorax may be regarded as made up of a *dorsal, lateral,* and *ventral zone*.

The meaning of the three zones of the thorax.—If the meaning of the three zones of the thorax be correctly grasped, a much clearer and truer conception of the mechanism of respiration will be obtained than by any other manner of regarding the costal series. Taking

first the meaning of the lateral segment, it will be seen that it is
concerned with the increase of the antero-posterior diameter of the
thorax.   Since the ribs decrease in length after the sixth or seventh,
then during inspiration, when the lower ribs are elevated, the antero-
posterior diameter of the lower part of the thorax is decreased—a fact
which may be verified in life.   The increase of obliquity from above
downwards   was   correctly   explained   in   the   classical   work   of
Hutchinson.   The external intercostal muscles which lie between the
lateral costal segments, the scalenus medius and anticus, are the
inspiratory muscles of the lateral segment of the thorax.   Since the
parts of the external intercostal sheet of muscle between the upper
intercostal spaces have the greater resistance to overcome in inspira-
tion, they have also a greater mechanical advantage in the more
horizontal position of the upper ribs.   The muscles of expiration of
the lateral zone of the thorax are (1) that part of the internal oblique
inserted to the ninth, tenth, and eleventh ribs; (2) the internal inter-
costals between the lateral segments of the ribs; (3) the external
oblique.   In normal respiration all these muscles are constantly in
action—the inspiratory overcoming in inspiration, the expiratory in
expiration.

The *dorsal* and *ventral* segments of the costal arcs are concerned
with the increase of the transverse diameter of the thorax, and are so
arranged as to bring about this effect.   The inspiratory muscle of the
ventral segment is the intercartilaginei; the expiratory, the triangularis
sterni and rectus abdominis.   The inspiratory muscles of the dorsal
segment are the exceeding strong external intercostal sheet between the
dorsal segments of the ribs, the levatores costarum, the scalenus
posticus, the serratus posticus superior, the cervicalis ascendens; and
perhaps the ilio-costalis should also be added.   The expiratory
muscles of the segment are the accessorius, serratus posticus inferior,
and quadratus lumborum.   By thus separating the thorax into three
zones, one obtains a rational explanation of the arrangement of the
respiratory muscles, and an easy way of teaching the mechanism of
respiration.

The mechanism of respiration in the orthograde primates contrasted
with that in the pronograde primates.—That in man, as in the
anthropoids, the thorax is peculiar in shape, the ribs peculiar in their
curvatures and flatness, the sternum peculiar in its breadth and
shortness, constitute a series of well-recognised facts.   Probably,
too, one may accept as approximately true that all of these characters
are in one way or another a result of the orthograde posture.   No
one, so far as I am aware, has ever sought to interpret the meaning of
these anatomical characters in so far as they indicate a modification
in the manner of respiration.   Here I merely wish to contrast a list
of the points in which respiratory mechanism of the orthograde
primates differs from that of the pronograde.   As far as regards the
general arrangement and composition of the three zones of the
thorax just described, the one form agrees with the other; also in the
arrangement of the intercostal muscles they agree.

I. As regards the Dorsal Zone of the Thorax.

Orthograde Primates.	Pronograde Primates.
a. Posterior costo-transverse ligaments, fibrous in structure.	a. The posterior costo-transverse ligaments are composed of yellow elastic tissue in the lower six ribs.
b. Quadratus lumborum, a wide sheet with ilio-costal fibres.	b. Quadratus lumborum, narrow series of inter-transverse fasciculi, no ilio-costal fibres being present in it.

II. As regards the Lateral Zone of the Thorax.

a. The scalenus medius ends on first rib.	a. Scalenus medius, strong inspiratory muscle reaching to the fourth or fifth rib.
b. The external oblique to the eleventh and twelfth ribs has an origin from the iliac crest.	b. The external oblique has no origin from the iliac crest.

III. As regards the Ventral Zone of the Thorax.

a. The triangularis sterni is in a state of retrogression.	a. The triangularis sterni is well developed.
b. No thoracic segment of the external oblique is present.	b. The external oblique extends forwards to the first rib.
c. The rectus abdominis ends on the lower set of ribs.	c. The rectus abdominis extends to the first rib and sternum.
d. Interchondral articulations may be present.	d. No interchondral articulations.
e. Seventh costal cartilage attached to and moves with the meso-sternum.	e. The seventh costal cartilages are attached to and move with the xiphi-sternum.

IV. As regards the Diaphragm.

a. The pericardium is adherent to the diaphragm.	a. The pericardium is separated from the diaphragm by the lobus azygos.
b. The spinal segment has a wide origin from the arcuate ligaments.	b. No arcuate origin or fibres are present.
c. The upper level of the diaphragm is approximately at right angles to the trunk.	c. The upper level of the diaphragm is nearly parallel to the ventral line of the belly.

Mr KEITH *exhibited the following models* : (1) one showing the manner in which the splenic flexure of the colon was displaced as the stomach emptied or filled ; (2) one showing the respiratory movements of the kidney ; (3) three models showing the respiratory movements of the liver, stomach, and spleen.

(2) *The Architecture of Bone illustrated by Röntgen Stereoscopy.* By W. S. HAUGHTON, Dublin, and A. FRANCIS DIXON, Cardiff.

As has been pointed out by Reiner and others, the architecture of the various bones of the skeleton can be beautifully demonstrated by

stereoscopic radiographs.   To obtain good results the specimens made use of may be macerated, or merely roughly cleaned.   Suitably-prepared lightly-printed photographic reproductions, when viewed in the reflecting stereoscope, illustrate very clearly the internal structure of the bone and the arrangement of the lamellæ of its cancellous tissue.   The whole effect is as if one were looking at a semi-transparent reconstruction of the bone.   The method has some advantages over the ordinary ground sections ; for instance, it enables one to follow with considerable ease the disposition of the lamellæ, even when they are constantly changing their direction, and lie in very different planes in different parts of their course.   Further, it is possible, by using large photographic plates, to obtain stereoscopic reproductions of the entire long bones, and also to obtain views illustrating the disposition of the lamellæ in planes at right angles to one another in the same specimen.   As the process is not a tedious one, in a relatively short time one can become possessed of reproductions illustrating the structure of the bones of the entire skeleton.   The pictures bring out clearly a system of spirally-arranged lamellæ common to all the long bones as well as the better-known longitudinal and transversely-arranged ones.   In all the long bones some of the lamellæ are seen forming right and left handed intersecting spirals.   These are particularly well marked in the femur and humerus, but are also present in all other bones of a tubular nature.   Where such bones are bent or curved, the spiral lamellæ are more strongly developed, and they undoubtedly give more rigidity to these parts.   In the ribs the spiral lamellæ are well seen, and they are also present in the transverse processes of the thoracic vertebræ and in the ends of the clavicle.   When the lamellæ in question are traced towards the articular ends of the long bones, they are noticed to undergo a change in direction, and to become perpendicular to the surfaces of pressure at the joints.

The reproductions of the vertebræ by the stereoscopic method are very beautiful, as the absence of dense bone renders it easy to obtain pictures showing, in its minutest detail, the disposition of the lamellæ and the changes in direction which they undergo near the surfaces of pressure, corresponding to the articular facets.   The ' pressure ' and ' tension lamellæ ' in the upper end of femur are shown very conspicuously.

A model illustrating diagrammatically the arrangement of the spiral lamellæ in the case of the femur was exhibited, and also a number of bone sections, to show their disposition.

In making the pictures, the apparatus devised by Dr M'Kenzie-Davidson of London was utilised.

(3) *On the Development of the Lower Ends of the Wolffian Ducts and Ureters and the Adjacent Parts of the Cloaca.* By Prof. A. ROBINSON.

The ureter arises as a bulbous diverticulum from the lower part of the Wolffian duct in embryos from three and a half to four weeks old, which possess a length of about 5·8 mm., and after its appearance the lower segment of the duct is known as the allantoic segment. The allantoic segment is common to both Wolffian duct and ureter, and it opens into a backward prolongation of the genito-urinary segment of the cloacal chamber, which may, for convenience, be termed the Wolffian angle. The allantoic segment persists until the embryo is 14 mm. long and about six weeks old ; then it disappears, and the Wolffian duct and the ureter open separately into the genito-urinary chamber. The exact manner in which the two canals attain their separate apertures and are afterwards moved apart until the ureter ends in the bladder section of the genito-urinary chamber, and the Wolffian duct, at a much lower level, into the genito-urinary canal, has never been fully elucidated; but it is generally believed that in the first place the allantoic segment of the Wolffian duct is absorbed into the genito-urinary chamber, and that, thereafter, on account of the rapid growth of the wall of the genito-urinary chamber between the orifices, the latter are forced apart. This may possibly be the correct explanation, but the sections of an embryo measuring 14·5 mm. in length, and presumably about seven weeks old, which has recently been added to my collection, suggest an alternative view. It should be noted, however, that I have not found a similar condition either in any other human embryo or in the embryos of other mammals. Possibly this particular embryo may be abnormal, but the features it presents are so distinct that they are worthy of note.

The dorsal and ventral sections of the cloaca are still continuous with each other, and neither opens on the surface. The ventral section, or genito-urinary chamber, is flattened dorso-ventrally, and in transverse section it is somewhat semilunar in outline at its widest part, which is in the region of the apertures of the Wolffian ducts and ureters. In this situation the lateral borders of the chamber are prolonged dorsally, forming what I have termed the Wolffian angles.

The ureter and the Wolffian duct on each side open close together into the corresponding Wolffian angle of the genito-urinary chamber, the former immediately to the outer side and slightly in front of the latter. So far, therefore, the specimen presents nothing which is opposed to the assumption that the allantoic segment of the Wolffian duct has been absorbed until the two canals have acquired separate apertures, but the point which is of importance is that from the posterior or lower margin of the orifice of the Wolffian duct a grooved ridge, the Wolffian ledge, runs caudally on the wall of the genito-urinary chamber, and gradually disappears at the junction of

the Wolffian angle with the body of the chamber.   The lateral margins of the groove are continuous anteriorly with the lateral margins of the aperture of the Wolffian duct, and apparently they fuse together to form the lower part of the ventral wall of the duct, which projects slightly into the cavity of the Wolffian angle of the chamber.   Obviously, if the lateral margins of the groove were to fuse from before backwards, the aperture of the Wolffian duct would be carried further backward in the chamber, and its distance from the opening of the ureter increased.   It may be supposed that after the fusion of the margins of the groove, the lower portion of the
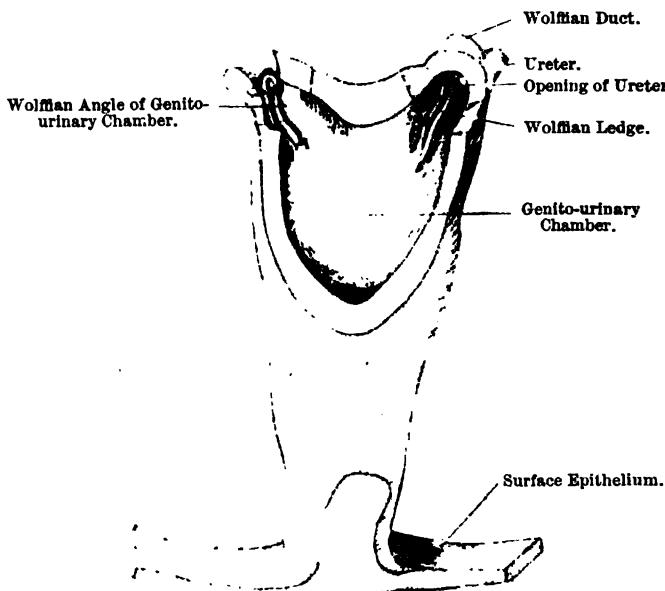
Reconstruction model of a human embryo 14·5 mm. long showing grooved ledges running downwards in the posterior wall of the genito-urinary chamber from the orifices of the Wolffian ducts.

Wolffian canal, which has thus been prolonged further backwards, separates from the wall of the genito-urinary chamber except at its lower extremity, and that consequently it enters the wall of the chamber, after the separation is completed, at a lower level than the ureter.

It is, of course, quite possible that the ridge and the sulcus are the remains of the allantoic segment of the Wolffian duct, in which case the Wolffian angle of the genito-urinary chamber must have been prolonged dorsally and forwards round the ventral wall of the duct, which would then project into the dorsal wall of the chamber; and it may be suggested that when this stage has been attained, the

ventral wall of the duct disappears, producing the condition found in this embryo. If this is the case, then the separation of the orifices of the ureter and the duct must be due entirely to the growth of the intervening part of the wall of the chamber into which both canals open. It should be noted, however, that in the specimen under consideration, the cavity of the Wolffian angle of the genito-urinary chamber extends forwards, along the ventral wall of the Wolffian duct, for a short distance beyond the point where the ureter and the duct open into the chamber.